# MIGRANT STOPOVER ECOLOGY AND RESIDENT RESILIENCE AFTER HURRICANE IRIS IN A NEOTROPICAL BIRD COMMUNITY

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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

May 2003

Abstract

I conducted two avian ecology studies in southern Belize. I examined mass gains by Nearctic-Neotropic migrants in forest near the Gulf of Honduras, a potential ecological barrier to migration. Condition indices (mass/wing chord or tail length) were used to estimate net diel mass gains in migrant species. Ten migrant species apparently were fattening at the site, but some species not fattening at the site had accumulated fat loads elsewhere, and this region appears to provide important resources for transient migrants.

I also studied the resilience of a marked resident bird community after Hurricane Iris severely altered the habitat. Given the severity of the disturbance, I expected that the bird community would have been severely impacted. Resident species were combined into ecological guilds, and patterns of captures and recaptures were compared before and after the hurricane. In resident species, survivors played an important role in the resilience of the community. Species abundances shifted, and the amount of fat that birds were carrying after the hurricane increased significantly. Despite the severe habitat alteration, local species extirpations were minimal, although the community was still changing one year after the storm.

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## Acknowledgements

This study was funded by the University of Alaska Museum, a USDA grant, an anonymous donor, and the University of Alaska Fairbanks Graduate School. I wish to thank the UA Museum, especially the Bird Lab, for the tremendous support I received during this project. My advisory committee, Dr. Abby Powell, Dr. Dana Thomas, and my graduate advisor Dr. Kevin Winker provided helpful advice during this project. The tireless editing of Dr. Winker improved this thesis immensely. Able field assistance was provided by Santos Hun for two field seasons, and Heather Moncrief during 2002. Critical support in Belize was provided by Don Owen-Lewis, the Francisca Bardalez family, the Hun family, Dr. Peter Dunham, Dr. Keith Prufer, and Wayne Bardalez. The personnel in the Conservation Division of the Forest Department in Belize provided the necessary permits to conduct the research, and working with them was a pleasure. Dr. David Johnson acted as my botanical consultant for the project.

General introduction

This thesis is comprised of two chapters treating ecological questions among migrant and resident birds in a second growth lowland forest edge in southern Belize. I went to the field to study migrant stopover ecology in a region that was likely to be very important to transient Nearctic-Neotropic migrants, and, as it turned out, I was able to collect enough data from multiple species to take a step forward in our understanding of Middle American migrations. I established a study site (1.26 ha) and operated 30 mist nets to study migrant stopover ecology at this site, asking the following questions: How much fat is carried by migrants in the region? Do migrants deposit fat at this site, and, if so, to what extent? Do migrants that have farther to travel fatten more? I compared my results with similar studies throughout North America to better understand the geographical patterns of fattening during migration and draw attention to this region as an important area to migrant fattening. Ten species were apparently depositing fat at the site, and some of those not depositing fat were already carrying substantial fat loads. This study was interrupted by Hurricane Iris, which struck on 8 October 2001. Despite the severe habitat alteration caused by Hurricane Iris, four of six species captured only after the hurricane showed significant daily mass gains.

In the process of netting over one thousand migrants, I had also netted nearly one thousand residents, and had established an individually marked resident community. When Hurricane Iris struck, I was at ground zero with a marked resident population and began to resample the site after the storm to answer the question: How did the resident bird community respond to this catastrophe? This data set is quite unique, and I am

unaware of another study that tracks the fate of a marked vertebrate community after severe habitat disturbance. Besides documenting changes in populations and community composition, I was particularly interested in the individuals present pre-hurricane and how they played a role in forming a new post-hurricane community. The results from the month of netting following Hurricane Iris were astounding. Overall capture rates increased, species losses were few, and, besides an invasion of open-habitat species, the forest community remained largely intact. Many banded birds remained on the study site, and fat scores of residents increased in the immediate post-hurricane sampling period. This apparent lack of change prompted a second year of study, and I returned in September 2002 to determine the fate of banded individuals and to assess the community change 11 months after Hurricane Iris struck. More changes had occurred since I last sampled at the site, and the overall capture rate decreased to pre-hurricane levels. More local extirpations occurred from the site, but this was countered by some new scrub-preferring species moving onto the site. Survivors were still present on the site, but they made up an even smaller proportion of the total population than they had immediately after the hurricane. Overall fat scores had increased even more. It was apparent that a new community was becoming established, one dominated by open-habitat preferring species. There was a corresponding loss of forest species and a reduction in populations. Thus, among forest species, not surprisingly, community resilience is a complex process that involved the species and individuals present before the disturbance and immigrants.

This study of the resilience in a Neotropical bird community after a catastrophic disturbance is the result of being in the wrong place at the right time, and is an example of the important role opportunistic studies can play in ecology.

Chapter 1: Catastrophic disturbance and resilience of a Neotropical bird community following Hurricane Iris

## 1.1 Abstract

As ecosystems become increasingly fragmented, remnant populations become isolated and have an increased risk of extinction. Natural disturbances increase the threat to remaining habitats, and there is a need to understand and manage for post-disturbance resilience. I examined the effects of a hurricane on a lowland Neotropical forest community of marked birds and assessed the contributions of survivors and immigrants to community resilience. I banded birds for 58 d prior to Hurricane Iris' impact (*Pre-Iris*: 11 August-7 October 2001), then resampled the plot for 28 d beginning 11 days after the storm (*Post-I*: 19 October-15 November 2001), and, finally, resampled again for 69 d beginning 11 months after Hurricane Iris (*Post-II*: 8 September-15 November 2002). I also sampled another site in 2002 outside the hurricane zone. Despite catastrophic habitat changes, the avian community seemed to be lightly impacted in Post-I. Species richness did not change significantly, and only five regularly occurring species were locally extirpated immediately in Post-I, although six more had been locally extirpated by Post-II. Species diversity declined significantly after Hurricane Iris. Forest species and all guilds but nectarivores showed significantly increased capture rates Post-I. Following this increase, only granivores did not decline in Post-II to significantly lower capture rates than Pre-Iris levels. Netting outside of the hurricane zone revealed that local extirpations were specific to it. Recapture rates were lower in Post-I than they were Pre-Iris. Recapture rates were lower after the hurricane (Post-I) than they had been before,

but survivors contributed to maintaining Post-I and Post-II populations and were, in some cases, the only representatives of a species on the site after Hurricane Iris.

**1.2 Introduction**

Efforts to preserve biodiversity increasingly manage isolated ecosystem fragments, such as parks, refuges, and reserves in a matrix of anthropogenically altered habitats. Natural disturbances are prominent worldwide, and most biological reserves will eventually incur a natural disturbance of some magnitude (Connell 1978, Sousa 1984, Scheffer et al. 2001). Managing for resilience, rather than managing to avoid disaster, is being promoted as the best approach to conservation objectives (Scheffer et al. 2001). The resilience of a community, its ability to absorb change without altering (Holling 1973), depends on the degree and extent of the disturbance, the persistence of its populations, recruitment through immigration and reproduction, and attributes of potential colonists (e.g., habitat preference, dispersal ability) from outside the disturbed area (Sousa 1984). An understanding of the contributions of survivors and immigrants to a community's resilience is required as habitat fragmentation increases and efforts to conserve biodiversity attempt to manage for resilience in natural populations. In vertebrate communities, we generally lack detailed data on these "seeds of resilience."

I examined resilience in an opportunistic study that used an unprecedented data set from a community of individually marked, nonmigratory (resident) Neotropical birds impacted by Hurricane Iris in southern Belize. Data from this natural trajectory experiment (*sic* Diamond 1986) provide the first glimpse at resilience on the level of marked individuals in a bird community, and allow us to examine the contributions that

survivors and immigrants make to rebuilding the post-catastrophe community. I used data on changes in population and community structure, individual capture-recapture data, and body condition to examine the early stages of recovery (immediate and one year later), and to elucidate the "seeds of resilience" at a level of detail not previously achieved.

**1.3 Study area and methods**

*1.3.1 Field methods*

My study site began as remnant primary forest joined with 25-year-old second-growth forest and edge adjacent to a citrus orchard in the floodplain of the Rio Grande near Big Falls, Toledo District, Belize (16° 15.82' N, 88° 52.37' W; Fig. 1.1). The site had a canopy height of approximately 20 m with some gaps, edge habitat filled with dense woody vegetation, and viny tangles of about 3 m in height. The study site was part of a regional matrix of habitats that included areas of pasture, milpa (slash and burn agriculture plots), and citrus orchard surrounded by tracts of lowland forest. K. Winker began working at this site during December 1997 with establishment of seven mist nets (12 x 2.6m) spaced 30 m apart over a 0.54 ha plot. The study continued during March of 1998 and 2001.

In August 2001 I extended the original study plot to include 30 mist nets spaced 30 m apart over a 1.26 ha plot. Nets were placed as two rows of 15, with mesh sizes alternating between 30 and 36 mm, and were opened all day (when conditions permitted) beginning on 11 August. I accrued 8,805 net h of sampling until 7 October, when nets were removed from the study plot in anticipation of Hurricane Iris, which struck on 8

October. Hurricane Iris ripped a 50 km-wide swath of destruction through southern Toledo District, Belize (Fig. 1.1). With sustained winds of 230 km/h and gusts approaching 300 km/h, the storm caused massive destruction, leaving extensive areas of lowland forest a tangle of fallen trees. The effect on the site was to change the habitat from a nearly closed-canopy forest of 20 m to a 5 m high tangle of uprooted and broken trees, branches, and vines (Fig. 1.2). On 19 October I re-opened 15 nets set on the same site in one row along the long axis of the plot. Five nets were placed back in their original net lanes, but placement of other nets was constrained by the drastically altered habitat (e.g., fallen trees and dense woody tangles). During this period, I only netted during the mornings and evenings due to the lack of shade on the plot and the detrimental effects of prolonged sun exposure on captured birds. I accrued another 1,114 net h until concluding the effort on 15 November.

I resampled the same plot from 8 September to 15 November 2002. The site was still a tangle of fallen woody vegetation 11 months after the hurricane, but the vegetation had completely greened over, and some of the few standing trees had leafed out, although others had died. Decay of downed woody debris had proceeded rapidly, and much of it had settled to the ground. For this resampling effort, I expanded the post-hurricane net grid to include 25 nets that covered most of the original plot, although due to habitat constraints nets were not as evenly spaced as they were before the hurricane struck. I sampled in the mornings only, usually closing nets by 1100, and accrued 2,784 net h. During October of this sampling period I established a control plot (Wayne's World) outside the hurricane zone (21 km south of the Big Falls site). Fourteen nets were placed

in three rows with 30 m spacing in a tract of second-growth forest similar in age and structure to what the Big Falls site had been before the storm. I sampled for 587 net h over 12 mornings at this plot, alternating between sites every 2 d.

Captured individuals (except hummingbirds) were marked using a numbered aluminum leg band. For hummingbirds, an outer rectrix was clipped. For each bird captured, time and net of capture were recorded, each bird was weighed to the nearest 0.1 gram on a Pesola spring scale, and scored for subcutaneous fat (following Helms and Drury 1960). Upon recapture, band number, net, and time were recorded. Aging criteria are generally not available for Neotropical residents (e.g., skull ossification is not usually a reliable criterion), so age data were not available for the autumn 2002 sampling period to distinguish between adult immigrants to the plot and juvenile recruitment.

*1.3.2 Data analyses*

Tropical communities are characterized by high species diversity but low numbers of any given species, and to increase statistical power I pooled species into foraging guilds based on Karr et al. (1990) and Stiles and Skutch (1989; Appendix 1.0). I also considered forest species as a group in the analyses, because these species were of special concern from a conservation perspective. Habitat preferences were based on personal observation, Jones and Vallely (2001) and Stiles and Skutch (1989; Appendix 1.0). I excluded migrant species due to their transience during the study periods. I defined my three sampling periods as ***Pre-Iris*** (11 August-7 October 2001); ***Post-I*** (19 October-15 November 2001); and ***Post-II*** (8 September-15 November 2002).

I used ranked abundance of the 15 most abundant species during each sampling period to examine changes in community structure (Karr et al. 1990). Shannon-Wiener diversity indices were calculated for the three sampling periods. I constructed species accumulation curves for each of the sampling periods and compared their shapes using Bonferroni-adjusted Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1981).

I examined changes in community structure by comparing the percentages that forest species and each guild contributed to the entire community using *G*-tests. I also excluded granivores, which are all open-habitat species at this site, and compared changes in the percentages that forest species and each guild contributed to the non-open-habitat community. Change in species richness was examined using a 2×3 *G*-test that compared species richness with the number of new captures. Change in species diversity was examined using Bonferroni-adjusted pairwise *t*-tests between samples (Zar 1999).

I did not use a mark-recapture technique to estimate population sizes during each sampling period, but instead I compared capture and recapture rates among sampling periods to examine changes in relative abundance and changes in recapture rates. The different habitat characteristics during the three sampling periods affected the capture probability by both increasing the percentage of vertical habitat sampled (Post-I and Post-II), and increasing movement rates (Post-I; see following). Recapture rates of marked individuals decline over time due to mortality and emigration, and the comparisons of recapture rates among different sampling periods that I made were designed to control for this expected decline.

I examined changes in capture rates among sampling periods in these groups by calculating a variance for the ratio of captures per net h during each sample period using equation 2.29 in Cochran (1963), and then used this variance to construct *t*-tests. I considered only morning captures (which was the only time of day sampled during all three sampling periods) from equal numbers of days of sampling in each sampling period to control for capture biases due to time of day and number of days sampled. For these capture rate analyses, banded individuals from a prior sampling period recaptured during a later period were considered as 'new captures'. They were counted as a recapture upon subsequent recapture during the same sampling period.

To test the effects of the hurricane on recapture rates, I compared the number of birds banded during Pre-Iris that were recaptured Post-I with the number of birds banded in the first half of the Pre-Iris sampling period that were recaptured in the second half of the Pre-Iris sampling period. Breaking the Pre-Iris sample into two periods this way served as a pre-hurricane control.

To examine year-to-year recapture rates, I compared the recapture rate of individuals banded in 1999 that were recaptured during 2001 (Pre-Iris and Post-I combined) with birds banded in 2001 (Pre-Iris and Post-I) that were recaptured during Post-II. I limited recapture rate comparisons between 2001 and 2002 to include only the three species banded in 1999 and recaptured in 2001. I define survivors as individuals banded Pre-Iris and then recaptured during Post-I or Post-II. I estimated the 'survivor component' during Post-I and Post-II as the percentage of all individuals on the plot that were survivors. The survivor component can be reduced by emigration or mortality of

banded individuals, immigration of unbanded individuals, and juvenile recruitment (Post-II only). The post-hurricane recapture of birds banded pre-Iris and the survivor component of the post-hurricane community measure different phenomena. Recapture of survivors measures persistence, whereas the survivor component considers this in addition to the level of immigration and juvenile recruitment, reflecting the contribution by the Pre-Iris community to the Post-I and Post-II communities at the level of the individual.

I examined changes in fat scores with a Kruskal-Wallis test for each group (all species, forest species, and guilds) over the three sampling periods. When there were significant differences among the three sampling periods, I used a Tukey-type nonparametric multiple comparison procedure to do pairwise comparisons between sampling periods to determine where those differences occurred (Zar 1999). Although the median fat score is the appropriate measure of central tendency for these ordinal data (Hailman 1965, but see Rogers 1991), I present mean fat scores because all median scores of resident species were zero, and the means allow a better understanding of the changes observed. Tests on fat scores were done at the guild and community levels, and no recaptures were included in these analyses.

To reduce the risk of making Type I errors, I minimized the number of tests conducted and used Bonferroni corrections where appropriate. Pairwise comparisons of capture rates were corrected for each group tested with $\alpha = 0.05/3 = 0.0167$. *G*-tests of independence were conducted with $\alpha = 0.05$ for 2×3 tests. Pairwise tests of recapture rates were conducted with $\alpha = 0.05$ for all groups. Kruskal-Wallis tests on fat scores for

each group were also conducted with $\alpha = 0.05$, and further Tukey pairwise comparisons were conducted with $\alpha = 0.05/3 = 0.0167$.

**1.4 Results**

I captured 102 resident species during this study; 44 species were captured during all 3 sampling periods. Fifty-five species were captured during both the Pre-Iris and Post-I sampling periods, 52 species were captured during both Pre-Iris and Post-II, and 47 species were captured during both Post-I and Post-II. Species richness was 78 Pre-Iris, 72 Post-I, and 62 Post-II. The declining values for species richness were not significantly different among sampling periods when compared to the number of captures in each sampling period ($G = 4.6$, $v = 2$, $P > 0.05$). The Shannon-Wiener species diversity index was 3.66 Pre-Iris, 3.10 Post-I, and 3.08 in Post-II. The Pre-Iris diversity was significantly higher than either the Post-I or Post-II diversity ($t$-values > 17, $v >$ 1000, $P < 0.001$), and Post-I was not significantly different from Post-II ($t = 0.6$, $v =$ 1238, $P > 0.05$).

Ranked abundance of the 15 most common species changed during each sampling period, but the most substantial changes occurred between the Pre-Iris and Post-I sampling periods (Table 1.1). This change was caused by a significant decline in the number of individuals of forest species as a percentage of the total community, and the Post-I and Post-II communities were dominated by granivores, which at this site were all open-habitat species (*Sporophila, Oryzoborus, Volatinia, Tiaris*; Table 1.2; Fig. 1.3). Omnivores did not change as a percentage of the community (Table 1.2; Fig. 1.3). Insectivores and frugivores changed significantly among sampling periods, declining as a

percentage of the community among all three sampling periods (Table 1.2; Fig. 1.3). The percentage of nectarivores also changed significantly, declining in Post-I, but increasing to near Pre-Iris levels during Post-II (Table 1.2; Fig. 1.3).

The Post-I species accumulation curve had a much higher intercept than the Pre-Iris curve, but their shapes were the same ($P > 0.1$; Fig. 1.4). The Post-II curve was significantly different than both the Pre-Iris and Post-I curves, climbing more steeply and flattening more abruptly than the other two ($P < 0.005$; Fig. 1.4).

The trend in capture rates among forest species and in all guilds except nectarivores and granivores was an increase from Pre-Iris levels during Post-I, and then a decrease to levels significantly below Pre-Iris during Post-II (Table 1.3). The capture rate of all species increased significantly during Post-I and declined to a level during Post-II that was not significantly different from the Pre-Iris rate (Table 1.3). In nectarivores, the Post-I capture rate was not significantly different from the Pre-Iris rate, but the Post-II rate was significantly lower than the Pre-Iris and Post-I rates (Table 1.3). The granivore capture rate increased significantly Post-I, then decreased during Post-II, but to levels above the Pre-Iris rate (Table 1.3).

Comparison of the within-Pre-Iris recapture rates with across-hurricane recapture rates (Pre-Iris to Post-I) showed significant declines for all species, forest species, and all guilds after the hurricane (Table 1.4). Of 38 birds of 3 species banded in 1999, nine (24%) were recaptured during 2001. Of 370 individuals of the same species banded during Pre-Iris and Post-I, 18 (5%) were recaptured during Post-II. These recapture rates were significantly different ($G = 13.26$, $v = 1$, $P < 0.005$), and this is a remarkable

difference: Recapture rates were higher over 29 months before the hurricane than in the same species over 11 months after the hurricane.

Recaptures of birds banded Pre-Iris were 15% during Post-I (Table 1.4, 'All banded species'), and by Post-II only 6% of birds banded Pre-Iris were recaptured (Table 1.4). Omnivores had the highest percentage of Post-I recaptures (23%), and granivores had the lowest (8%; Table 1.4). Granivores had the highest recapture rate Post-II (10%), and frugivores had the lowest (2%; Table 1.4). Among forest species, the percentage of Pre-Iris birds recaptured during Post-I was 18%, but then dropped to 5% during Post-II (Table 1.4).

The Post-I survivor component of the community (the percentage of individuals in the Post-I sample that had been banded Pre-Iris) for all species was 15% (Table 1.4). The Post-I guild-level survivor component was lowest in granivores (4%), highest in insectivores (41%), and among forest species was 25% (Table 1.4). During Post-II, the survivor component of all species was 10% (Table 1.4). At the guild level, the Post-II survivor component was lowest in omnivores (9%), and highest in insectivores and frugivores (18%; Table 1.4). The Post-I survivor component among forest species was 25%, but this dropped to 15% by Post-II (Table 1.4).

Omnivores and frugivores changed significantly as a proportion of the non-granivore community (Table 1.5; Fig. 1.5). Omnivores declined during Post-I, but increased to Pre-Iris proportions during Post-II (Table 1.5; Fig. 1.5). Frugivores maintained their proportion of the non-granivore community in Post-I, but then declined in Post-II (Table 1.5; Fig. 1.5).

Sixty-six percent of species banded Pre-Iris were represented by survivors in Post-I, and 40% of species banded Pre-Iris were represented by survivors in Post-II (Appendix 1.0). In species with more than one individual banded Pre-Iris, the highest recapture level during Post-I was 83% *(Thamnophilus doliatus)*, and none of the ten species with the highest recapture level were open-habitat species (Appendix 1.0). During Post-II, the highest recapture level in a species was 33% (*Tolmomyias sulfurescens*), and of the ten species with the highest recapture levels, only one was an open-habitat species (*Oryzoborus funereus*; Appendix 1.0).

The Post-I survivor component for species in which more than one individual was banded Pre-Iris was highest in *Synallaxis erythrothorax* and *Saltator maximus*, (both 100%) and the ten species with the highest survivor component included no open-habitat species (Appendix 1.0). The ten species with the highest Post-II survivor component for which more than one individual was banded Pre-Iris was again highest in *Synallaxis erythrothorax* (50%) and again included the same open-habitat species (*Oryzoborus funereus*; Appendix 1.0).

The presence of a species during Post-I was not strongly dependent upon the presence of survivors; nine of 16 species (56%) not represented by any survivors were still captured on the site during Post-I (Appendix 1.0). This pattern was similar during Post-II, and 18 of 30 species (60%) that had no survivors were still captured during Post-II (Appendix 1.0). Recapture during Post-I was a good predictor of species presence during Post-II, and of 32 species that were recaptured during Post-I, only five (16%) were locally extirpated from the site by Post-II (Appendix 1.0). A species' detection by Post-I

was a good predictor of detection during Post-II; *Saltator atriceps* was the only one of six species not captured during Post-I that was captured during Post-II (Appendix 1.0).

The species with the highest levels of recaptures and highest survivor components were those often associated with edges or second growth scrub (e.g., *Synallaxis erythrothorax*, *Thamnophilus doliatus*), although many forest species also showed values nearly as high (Appendix 1.0).

Most species caught only during Pre-Iris were represented by fewer than five individuals. However, species captured regularly Pre-Iris that were absent in the Post-I sample were *Phaethornis longuemareus, Dendrocincla homochroa, Onychorhynchus mexicanus, Schiffornis turdinus,* and *Henicorhina leucosticta* (Appendix 1.0). Several more species regularly captured during Pre-Iris locally extirpated by Post-II were *Phaethornis superciliosus, Xenops minutus*, *Gymnocichla nudiceps*, *Hylophilus ochraceiceps, Euphonia gouldi,* and *Arremon aurantiirostris* (Appendix 1.0).

I captured 113 individuals of 33 species outside the hurricane zone at Wayne's World, including species that were locally extirpated or suffered severe reductions in population on the main site following the hurricane(e.g., *Phaethornis superciliosus*, *Xenops minutus*, *Dendrocincla homochroa*, *Mionectes oleagineus,* and *Henicorhina leucosticta*).

Community energetics also seemed to be affected by the hurricane. Fat scores of the entire avian community increased significantly during Post-I (Table 1.6). This was driven by fat score increases in forest species, omnivores, and frugivores; insectivores and granivores did not show significant increases during Post-I (Table 1.6). During Post-

II, mean fat scores showed another significant increase at the community level, and insectivore and granivore fat scores also increased significantly from Pre-Iris levels (Table 1.6). Fat levels among forest species, omnivores, and frugivores decreased between Post-I and Post-II, but only frugivores decreased to near Pre-Iris levels (Table 1.6).

**1.5 Discussion**

Understanding the details of resilience after a disturbance requires pre- and post-disturbance data from a marked community. Our data provide the first glimpse of these details in a vertebrate community and show that community response to such a catastrophe is complex, resulting in changes in community structure, but not necessarily through the widespread local extirpations of species or individuals that might be expected given the catastrophic habitat changes. Survivors appeared to play an important role in the recovery of this community.

Resilience after catastrophic disturbances has been best studied in plants, and in some forests after hurricanes regeneration occurred directly from survivors, through the resprouting of stumps or roots, rather than through the establishment of pioneer communities (Whigham et al. 1991, Yih et al. 1991, Bellingham et al. 1992). However, other hurricane studies reported substantial levels of recruitment of early-successional species (Frangi and Lugo 1991, Walker 1991). Direct mortality of marked trees in Jamaica due to a hurricane was higher than in non-hurricane years, but not catastrophic (Bellingham et al. 1992), and none of these studies predicted any major plant community shifts due to the disturbances.

The mobility of animals makes it more difficult to study their resilience (Sousa 1984), and until this study there have been no detailed pre-disturbance data sets from marked animal communities that allow comparison with post-disturbance changes. Five of six large terrestrial rainforest invertebrates (gastropods and insects) suffered significant declines after Hurricane Hugo struck Puerto Rico, and three of those species appeared to have been locally extirpated from the study site eight months after the hurricane struck (Willig and Camilo 1991). *Anolis* lizards and adult frogs in Puerto Rico were able to persist for 18 months after Hurricane Hugo without apparent changes in populations (Reagan 1991, Woolbright 1991). On small Caribbean islets that were inundated by a storm surge, the survival of eggs was critical to the resilience of *Anolis* lizard populations (Schoener et al. 2001).

In birds, most hurricane data come from Caribbean islands and adjacent mainland sites in Mexico and northern Central America (Askins and Ewert 1991, Lynch 1991, Waide 1991, Will 1991, Wauer and Wunderle 1992, Wunderle et al. 1992, Wunderle 1995). These studies focused on population trends, and presented data on population changes over time. No data on the fates of survivors were presented, although many of these studies used mist netting to estimate relative abundances of birds. Like many of these studies, Hurricane Iris caused population reductions in forest-associated species (Table 3). It also promoted an invasion of granivorous species into the formerly forested area, causing the percentage of the community that was granivorous to more than double between the Pre-Iris and Post-II periods (Table 2; Fig. 4). Askins and Ewert (1991) also

noted an invasion of a granivore, *Tiaris bicolor,* after Hurricane Hugo struck St. John, U. S. Virgin Islands.

It is likely that the decrease in recaptures at our site between Pre-Iris and Post-I (Table 1.4) was due to higher levels of movement (emigration and immigration), rather than direct hurricane mortality (Sutton 1945), and the increase in capture rates among all groups during Post-I also supports low direct mortality due to the storm (Table 1.3).

Five species that were captured regularly during Pre-Iris were locally extirpated Post-I (*Phaethornis longuemareus, Dendrocincla homochroa, Onychorhynchus mexicanus, Schiffornis turdinus,* and *Henicorhina leucosticta;* Appendix 1.0). This seemingly low species loss, combined with a large number of recaptures of survivors, suggested that Post-I resilience was phenomenal in contrast to the catastrophic physical changes that the habitat showed (Fig. 1.2). Species retention during Post-I was remarkable, but although my data do not indicate a significant change in species richness at the site, there was a substantial shift in community structure, demonstrated by changes in species diversity, ranked abundance changes (Table 1.1) and in changes in the proportions of guilds and forest species with respect to the entire community (Tables 1.2 and 1.5).

The significant change in the shape of the Post-II species accumulation curve (Fig. 1.4) also suggested a change in community dynamics compared to previous sampling periods. The Post-II curve was initially steeper, but then flattened out more abruptly than the Pre-Iris or Post-I curves, which were not as steep, and flattened out more smoothly (Fig. 1.4). This steep initial increase of the Post-II curve suggests that the

species present in the Post-II habitat may have been more vulnerable to capture than in the previous two sampling periods. The abrupt change in slope is probably due to fewer rare species on the site.

A strong stirring effect and a period of transience in the Post-I community caused by Hurricane Iris is suggested by the higher capture rates (Table 1.3) and lower recapture rates (Table 1.4) during Post-I. During Post-II, capture rates declined to levels significantly lower than those during Pre-Iris in most groups (Table 1.3), suggesting that changes were continuing. Population reductions were evident from the lower capture rates during Post-II (Table 1.3), and these reductions must have been substantial, because a lowered canopy alone should have increased capture rates. Stouffer and Bierregaard (1995) also noted that the year following disturbance in lowland Amazonian forest was characterized by higher capture rates in small forest fragments before the populations of many forest species decreased to below pre-disturbance levels.

Granivores and the frugivore *Pipra mentalis* showed a pronounced immediate population increase during Post-I (Table 1.4), and most new species on the site during Post-I were canopy species that were probably present above the nets during Pre-Iris sampling (e.g., *Ornithion semiflavum, Tityra semifasciata*, and *Chlorophanes spiza*).

Delayed effects of Hurricane Iris were apparent for many species, and seven species that were common during Pre-Iris were not captured during Post-II (*Phaethornis longuemareus, P. superciliosus*, *Xenops minutus*, *Gymnocichla nudiceps*, *Henicorhina leucosticta*, *Euphonia gouldi,* and *Arremon aurantiirostris;* Appendix 1.0; although *P. longuemareus* and *Arremon* were observed on the plot). Others (e.g., *Mionectes*

*oleagineus*) were severely reduced in abundance (Appendix 1.0). Post-II also revealed a delayed arrival of some new immigrants to the plot (e.g., *Columbina talpacoti* and *Anthracothorax prevostii*).

The increase in subcutaneous fat loads in the resident community suggests that the storm affected avian community energetics. Wunderle (1995) found an increase in average mass and higher fat scores in some bird species after a hurricane in Puerto Rico. He attributed increased mass in *Coereba flaveola* to differential selection favoring larger-bodied birds and the immigration of larger-bodied birds from the highlands, where they are known to be heavier. Although I do not discount Wunderle's hypothesis, I believe that fat scores were higher after Hurricane Iris because individuals were probably "insurance fattening" to compensate for resource uncertainty in the highly altered environment. Higher fat loads in Greenish Leaf Warblers (*Phylloscopus trochiloides*) wintering in tropical India were attributed to low prey availability due to lack of rainfall (Katti and Price 1999), and the higher fat scores observed during Post-II suggest that there is still a higher degree of resource uncertainty in the hurricane-altered habitat even one year later. It is important to note that there apparently were enough resources available to sustain this fattening despite the catastrophic habitat changes.

By Post-II, resilience in this community resulted from a combination of survivors and some mix of immigrants and juvenile recruits. Juvenile recruitment Post-II almost certainly played a role, but too little is known about aging Neotropical residents to examine the importance of recruitment to resilience here. These data show that the presence of a species during Post-I or Post-II was not entirely dependent upon survivors

(except *Synallaxis erythrothorax* and *Saltator maximus* Post-I, in which the only individuals present were survivors; Appendix 1.0). The presence or absence of a species during Post-I was a good predictor of its presence or absence Post-II. Sixty-six percent of species present in Post-I were represented partly by survivors. This percentage dropped to 40% by Post-II, but a reduction would be expected due to mortality. These survivors comprised a small but important percentage of the Post-I and Post-II communities. Such a high percentage of species with survivors might not have been predicted given the extensive damage by Hurricane Iris, and in some instances survivors were the only representatives of a species on the plot (e.g., *Synallaxis erythrothorax*).

This study of the responses of marked individuals to a hurricane has shown that some effects on the community were immediate, such as increased capture rates, losses of some species, the increase of open-habitat species, and an increase in canopy species. There were also important delayed effects that were not evident until one year later during Post-II. Populations were significantly reduced in most guilds (except granivores) to below Pre-Iris levels, and more species that were relatively common Pre-Iris had been lost from the site by Post-II than Post-I. Immigration of some new species onto the site was not detected until Post-II.

Despite catastrophic habitat changes and shifts in community structure, there were no significant losses in species richness, although species diversity declined significantly after Hurricane Iris. Species loss occurred during both Post-I and Post-II, but this was offset in Post-I by remaining canopy species and in Post-II by immigrants that preferred scrub-type habitats. Decreased capture rates, indicating declining populations, make it

likely that additional losses of forest species will occur on the site as the community continues to change. Many species were represented by survivors during both the Post-I and Post-II sampling periods, and survivors played an important role in the resilience of the community.

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Table 1.1. Ranked abundance (and sample sizes) for the 15 most abundant species in each sampling period.

| Species | Rank (*N*) | | | | | |
|---|---|---|---|---|---|---|
| | Pre-Iris | | Post-I | | Post-II | |
| *Sporophila aurita* | 1 | (141) | 2 | (115) | 2 | (101) |
| *Mionectes oleagineus* | 2 | (121) | 3 | (67) | 15 | (5) |
| *Manacus candei* | 3 | (93) | 4 | (49) | 6 | (17) |
| *Amazilia tzacatl* | 4 | (43) | 15 | (9) | 4 | (23) |
| *Oryzoborus funereus* | 5 | (35) | 6 | (35) | 3 | (27) |
| *Ramphocelus passerinii* | 6 | (31) | 5 | (41) | 7 | (15) |
| *Phaethornis superciliosus* | 7 | (30) | 22 | (2) | – | |
| *Cercomacra tyrannina* | 8 | (27) | 12 | (13) | 14 | (6) |
| *Thryothorus maculipectus* | 9 | (25) | 14 | (11) | 8 | (14) |
| *Sporophila torqueola* | 10 | (24) | 1 | (219) | 1 | (144) |
| *Synallaxis erythrothorax* | 11 | (20) | 22 | (2) | 16 | (4) |
| *Turdus grayi* | 12 | (18) | 7 | (29) | 10 | (10) |
| *Todirostrum sylvia* | 13 | (16) | 22 | (2) | 15 | (5) |
| *Xiphorhynchus flavigaster* | 13 | (16) | 16 | (8) | 17 | (3) |
| *Henicorhina leucosticta* | 13 | (16) | – | | – | |
| *Saltator maximus* | 14 | (15) | 20 | (4) | 10 | (10) |
| *Amblycercus holosericeus* | 14 | (15) | 21 | (3) | 14 | (6) |
| *Tolmomyias sulfurescens* | 15 | (14) | 13 | (12) | 14 | (6) |
| *Formicarius analis* | 15 | (14) | 19 | (5) | 17 | (3) |

Table 1.1. (continued)

| Species | Rank (*N*) | | | | | |
|---|---|---|---|---|---|---|
| | Pre-Iris | | Post-I | | Post-II | |
| *Attila spadiceus* | 15 | (14) | 19 | (5) | 17 | (3) |
| *Eucometis penicillata* | 15 | (14) | 23 | (1) | 18 | (2) |
| *Pipra mentalis* | 15 | (14) | 8 | (27) | 19 | (1) |
| *Arremonops chloronotus* | 16 | (13) | 21 | (3) | 12 | (8) |
| *Leptotila cassinii* | 16 | (13) | 19 | (5) | 15 | (5) |
| *Thamnophilus doliatus* | 17 | (12) | 17 | (7) | 13 | (7) |
| *Dendrocincla anabatina* | 17 | (12) | 15 | (9) | 14 | (6) |
| *Volatinia jacarina* | 18 | (11) | 10 | (17) | 5 | (22) |
| *Ramphocaenus melanurus* | 18 | (11) | 17 | (7) | 9 | (12) |
| *Coereba flaveola* | 18 | (11) | 9 | (20) | 12 | (8) |
| *Veniliornis fumigatus* | 20 | (9) | 20 | (4) | 15 | (5) |
| *Myiopagis viridicata* | 21 | (7) | 17 | (7) | 11 | (9) |
| *Habia fuscicauda* | 21 | (7) | 13 | (12) | 15 | (5) |
| *Taraba major* | 23 | (5) | 21 | (3) | 15 | (5) |
| *Tiaris olivacea* | 25 | (3) | 11 | (14) | 10 | (10) |
| Total *N* | | (865) | | (767) | | (507) |

– =Absent in sample period.

Table 1.2. Community composition by habitat preference and guild during each sampling period.

| | *N* (%) |
|---|---|
| ***Forest Species**** | |
| Pre-Iris | 654 (62) |
| Post-I | 372 (43) |
| Post-II | 178 (31) |
| ***Insectivores**** | |
| Pre-Iris | 334 (31) |
| Post-I | 156 (18) |
| Post-II | 112 (20) |
| ***Omnivores*** | |
| Pre-Iris | 151 (14) |
| Post-I | 121 (14) |
| Post-II | 72 (13) |
| ***Frugivores**** | |
| Pre-Iris | 247 (23) |
| Post-I | 148 (17) |
| Post-II | 43 (8) |

Table 1.2. (continued)

| | *N* (%) |
|---|---|
| ***Nectarivores**** | |
| Pre-Iris | 105 (10) |
| Post-I | 39 (5) |
| Post-II | 43 (8) |
| ***Granivores**** | |
| Pre-Iris | 219 (21) |
| Post-I | 400 (46) |
| Post-II | 303 (53) |

* Denotes significant difference among sampling periods at $\alpha = 0.05$.

Table 1.3. Comparisons of morning capture rates (captures/net h) during each sampling period.[1]

| | *N* | Mean | SD |
|---|---|---|---|
| ***All species*** | | | |
| Pre-Iris | 373 | 0.2047[a2] | 0.0348 |
| Post-I | 712 | 0.7993[b] | 0.0542 |
| Post-II | 338 | 0.2098[a] | 0.0216 |
| ***Forest species*** | | | |
| Pre-Iris | 292 | 0.1602[a] | 0.0289 |
| Post-I | 345 | 0.3873[b] | 0.0525 |
| Post-II | 144 | 0.0894[c] | 0.0119 |
| ***Insectivores*** | | | |
| Pre-Iris | 141 | 0.0774[a] | 0.0140 |
| Post-I | 128 | 0.1437[b] | 0.0204 |
| Post-II | 75 | 0.0465[c] | 0.0060 |
| ***Omnivores*** | | | |
| Pre-Iris | 68 | 0.0373[a] | 0.0076 |
| Post-I | 148 | 0.1662[b] | 0.0198 |
| Post-II | 51 | 0.0316[c] | 0.0056 |
| ***Frugivores*** | | | |
| Pre-Iris | 44 | 0.0241[a] | 0.0047 |
| Post-I | 60 | 0.0674[b] | 0.0139 |
| Post-II | 20 | 0.0124[c] | 0.0032 |

Table 1.3. (continued)

| | *N* | Mean | SD |
|---|---|---|---|
| ***Nectarivores*** | | | |
| Pre-Iris | 58 | 0.0318[a] | 0.0069 |
| Post-I | 31 | 0.0348[a] | 0.0069 |
| Post-II | 29 | 0.0180[b] | 0.0052 |
| ***Granivores*** | | | |
| Pre-Iris | 133 | 0.0730[a] | 0.0169 |
| Post-I | 336 | 0.3772[b] | 0.0478 |
| Post-II | 164 | 0.1018[c] | 0.0100 |

[1] Capture rates are from mornings only because it was the only time of day sampled during all three sampling periods.

[2] Sampling periods with the same letter are not significantly different from each other at $\alpha = 0.05/3$.

Table 1.4. Tracking survivors by guilds and groups: Fates of individuals banded before Hurricane Iris that were recaptured during subsequent sampling periods.

| Species | Banded first half Pre-Iris | Recaptured second half Pre-Iris (%) | Total banded Pre-Iris | Recaptured Post-I (%)[1] | Recaptured Post-II (%)[1] | Total captured Post-I | Post-I survivor composition (%)[2] | Total captured Post-II | Post-II survivor composition (%)[2] |
|---|---|---|---|---|---|---|---|---|---|
| ***All banded species**** | 375 | 92(25) | 768 | 118(15) | 49(6) | 769 | 15 | 491 | 10 |
| ***Forest species**** | 246 | 69(28) | 525 | 93(18) | 25(5) | 371 | 25 | 178 | 14 |
| ***Insectivores*** | 116 | 40(34) | 213 | 46(22) | 18(8) | 113 | 41 | 101 | 18 |
| ***Omnivores*** | 70 | 8(11) | 116 | 27(23) | 5(4) | 104 | 26 | 58 | 9 |
| ***Frugivores**** | 75 | 24(32) | 227 | 28(12) | 5(2) | 145 | 19 | 28 | 18 |
| ***Granivores**** | 112 | 19(17) | 206 | 16(8) | 21(10) | 384 | 4 | 294 | 7 |

[1] Percentage of birds banded during Pre-Iris that were recaptured during period.

[2] Percentage of birds captured during period that had been banded Pre-Iris.

* Denotes significant difference in recapture rate between "Recaptured second half Pre-Iris (%)" and "Recaptured Post-I (%)" at $\alpha = 0.05$.

Table 1.5. Percentages of groups that made up the non-granivore captures. Letters indicate which groups are significantly different at $\alpha = 0.05$.

| | *N* (%) |
|---|---|
| ***Forest Species*** | |
| Pre-Iris | 654(77) |
| Post-I | 372(80) |
| Post-II | 178(65) |
| ***Insectivores*** | |
| Pre-Iris | 334(40) |
| Post-I | 156(34) |
| Post-II | 112(41) |
| ***Omnivores**** | |
| Pre-Iris | 151(33) |
| Post-I | 121(14) |
| Post-II | 72(27) |
| ***Frugivores**** | |
| Pre-Iris | 247(29) |
| Post-I | 148(32) |
| Post-II | 43(16) |

Table 1.5. (continued)

| | *N* (%) |
|---|---|
| ***Nectarivores*** | |
| Pre-Iris | 105(12) |
| Post-I | 39(8) |
| Post-II | 43(16) |

* Denotes significant difference among sampling periods at $\alpha = 0.05$.

Table 1.6. Changes in fat scores. Letters indicate which means are significantly different at $\alpha = 0.05$.

| Guild | *N* | Mean fat score |
|---|---|---|
| ***All Species****** | | |
| Pre-Iris | 610 | 0.192[a] |
| Post-I | 653 | 0.326[b] |
| Post-II | 261 | 0.463[c] |
| ***Forest species****** | | |
| Pre-Iris | 405 | 0.212[a] |
| Post-I | 263 | 0.546[b] |
| Post-II | 55 | 0.382[b] |
| ***Insectivores**** | | |
| Pre-Iris | 162 | 0.0864[a] |
| Post-I | 75 | 0.187[b] |
| Post-II | 20 | 0.25[b] |
| ***Omnivores****** | | |
| Pre-Iris | 86 | 0.0698[a] |
| Post-I | 74 | 0.5[b] |
| Post-II | 23 | 0.435[b] |

Table 1.6. (continued)

| Guild | *N* | Mean fat score |
|---|---|---|
| ***Frugivores****** | | |
| Pre-Iris | 185 | 0.362[a] |
| Post-I | 107 | 0.748[b] |
| Post-II | 16 | 0.5[a,b] |
| ***Granivores****** | | |
| Pre-Iris | 175 | 0.16[a] |
| Post-I | 378 | 0.172[a] |
| Post-II | 200 | 0.485[b] |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

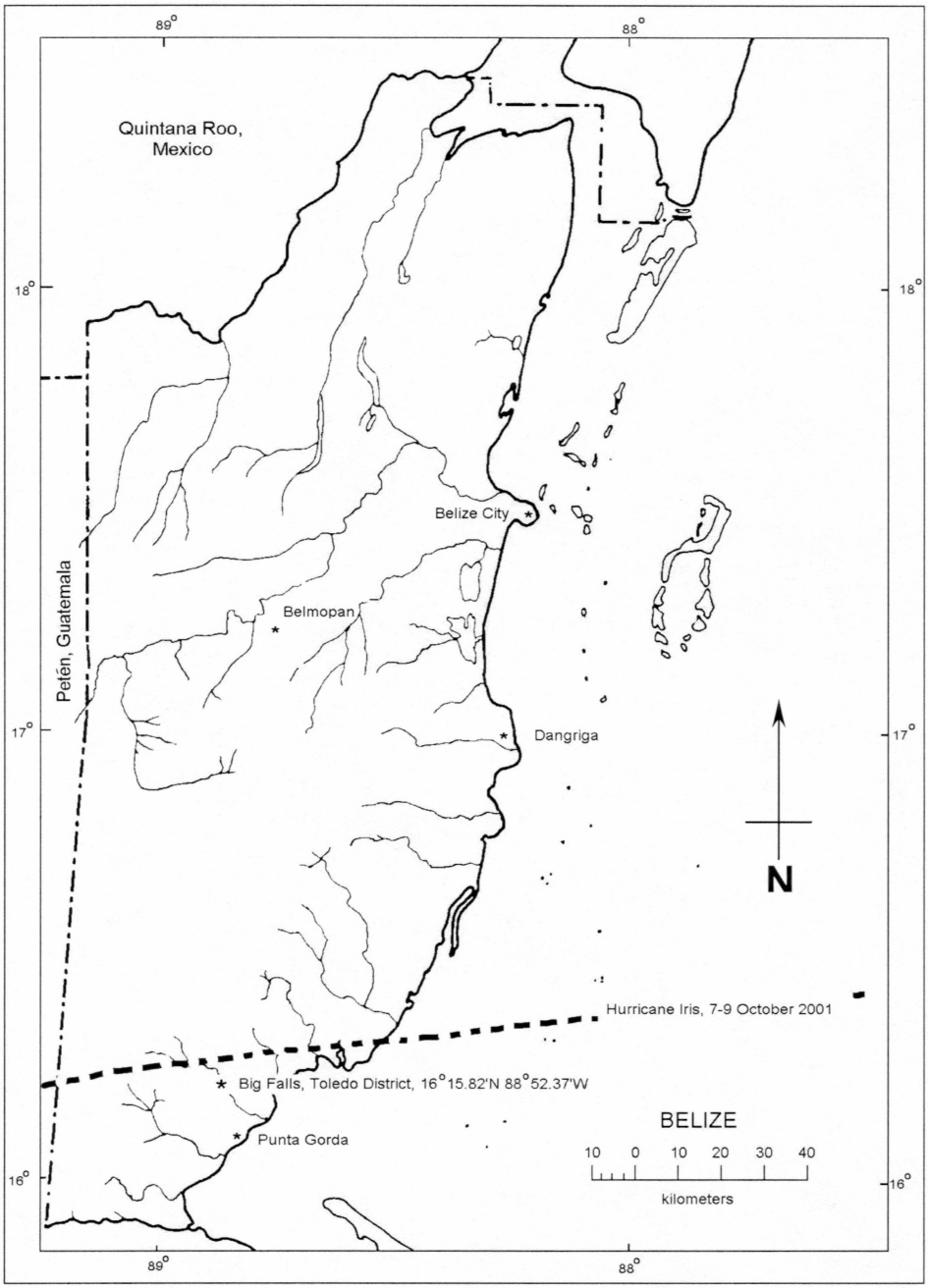


Figure 1.1. Map of Belize showing location of the study site and the path of Hurricane Iris. (modified from Russell 1964).

Figure 1.2. Habitat change caused by Hurricane Iris on 8 October 2001 in Big Falls, Toledo District, Belize. Top: Pre-Iris; bottom: Post-I.

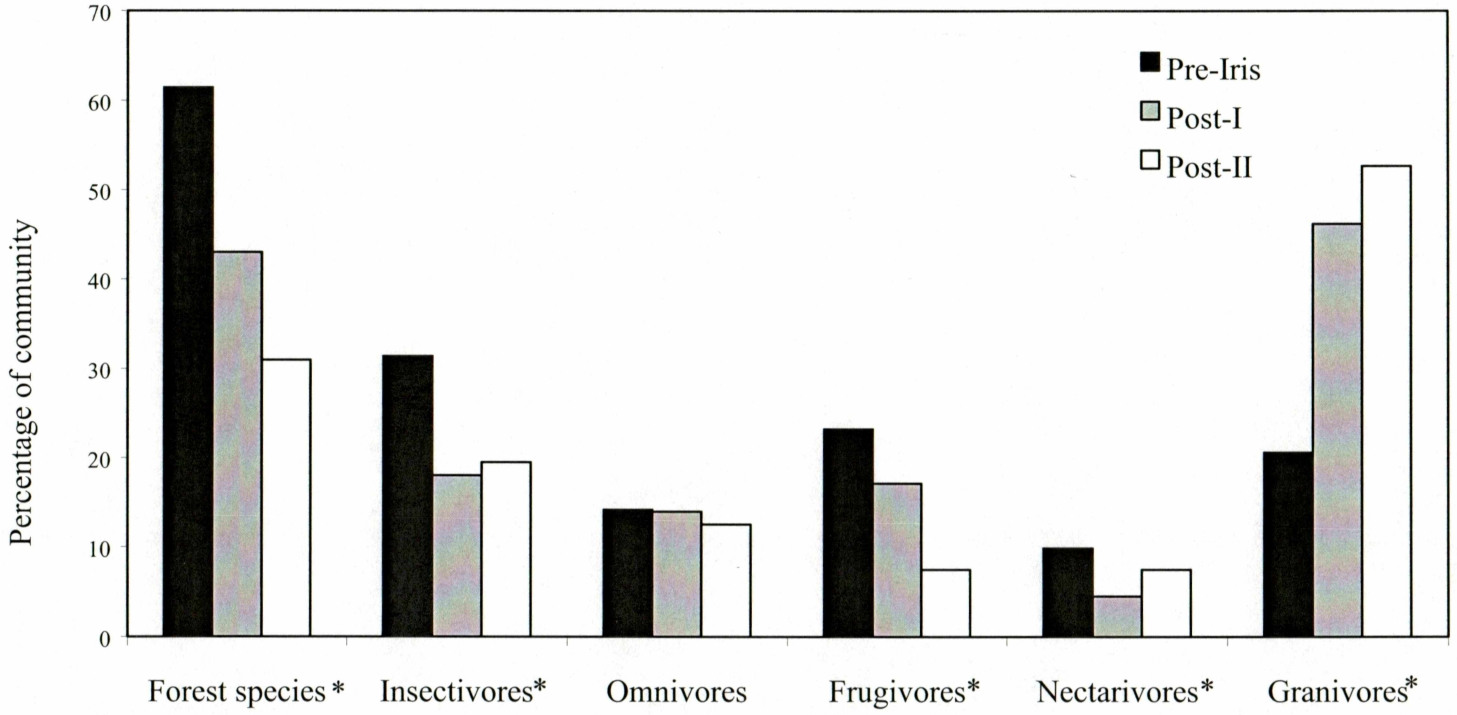


Figure 1.3. Community composition by habitat preference and guild during each sampling period.

* Indicates significant differences among sampling periods.

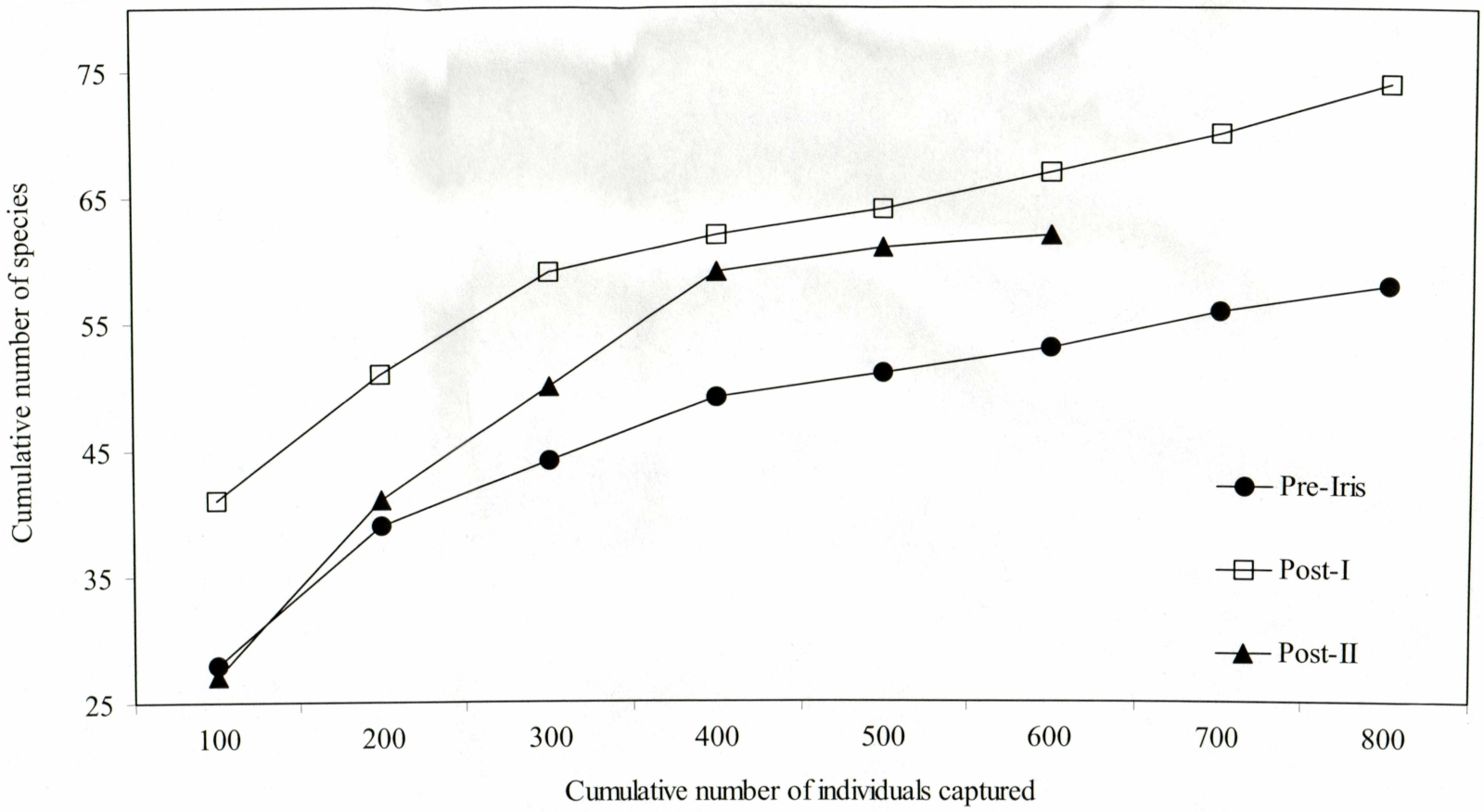


Figure 1.4. Species accumulation curves during the three sampling periods to contrast changes in community structure among them.

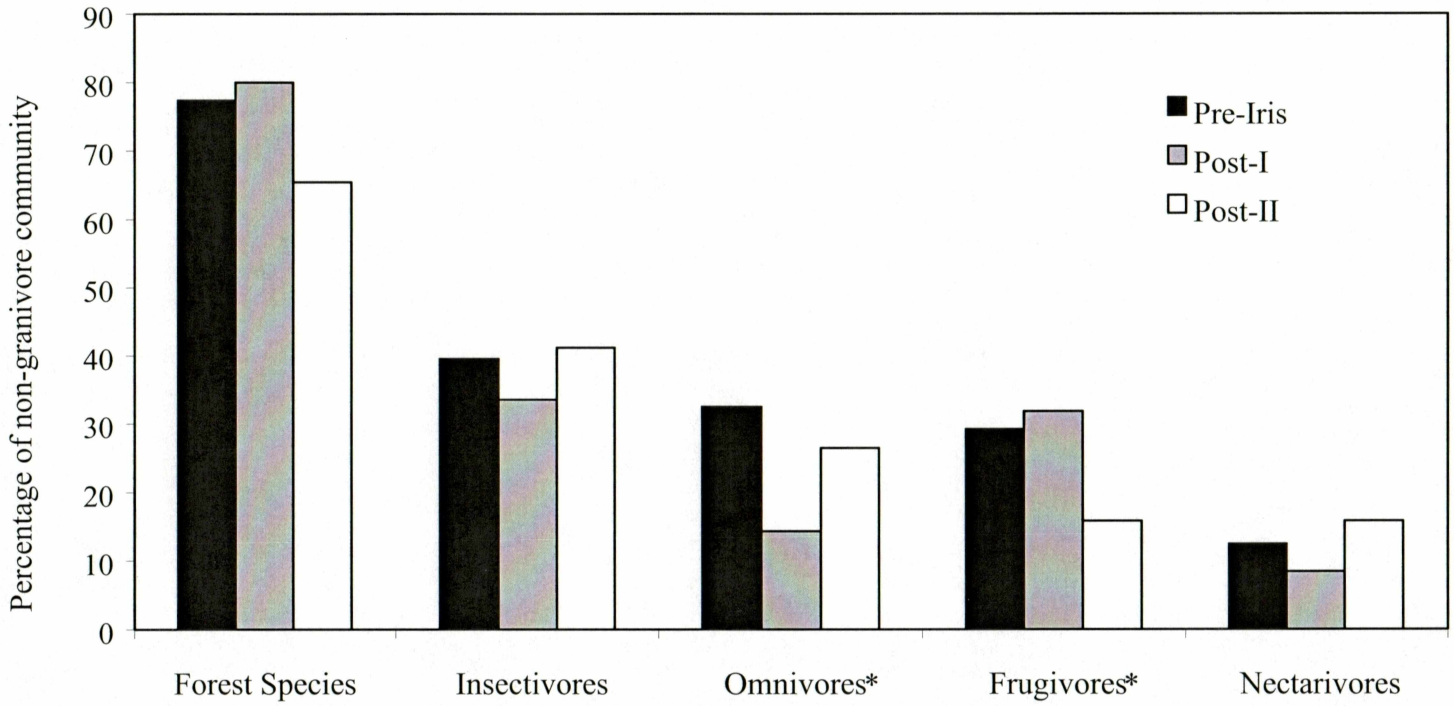


Figure 1.5. Percentages of groups that made up the non-granivore captures.

* Indicates significant differences among sampling periods.

Appendix 1.0. Tracking survivors by species[1,2]: Fates of individuals banded before the hurricane that were recaptured during subsequent sampling periods.

| Species | Total banded Pre-Iris | Recaptured Post-I (%) | Recaptured Post-II (%) | Total captured Post-I | Post-I survivor composition (%) | Total captured Post-II | Post-II survivor composition (%) |
|---|---|---|---|---|---|---|---|
| *Leptotila cassini*[FF] | 6 | 1(17) | 1(17) | 5 | 20 | 5 | 20 |
| *Phaethornis longuemareus*[FN,3] | 7 | | | 0 | | 0 | |
| *Phaethornis superciliosus*[FN,3] | 30 | | | 2 | | 0 | |
| *Amazilia tzacatl*[SN,3] | 43 | | | 9 | | 23 | |
| *Amazilia candida*[FN,3] | 10 | | | 6 | | 5 | |
| *Chloroceryle aenea*[FP] | 2 | 0(0) | 0(0) | 3 | 0 | 2 | 0 |
| *Pteroglossus torquatus*[FO] | 1 | 0(0) | 0(0) | 1 | 0 | 0 | |
| *Veniliornis fumigatus*[FI] | 6 | 3(50) | 1(17) | 4 | 75 | 5 | 20 |
| *Melanerpes aurifrons*[SI] | 1 | 0(0) | 0(0) | 0 | | 0 | |
| *Synallaxis erythrothorax*[SI] | 19 | 2(11) | 2(11) | 2 | 100 | 4 | 50 |

Appendix 1.0. (continued)

| Species | Total banded Pre-Iris | Recaptured Post-I (%) | Recaptured Post-II (%) | Total captured Post-I | Post-I survivor composition (%) | Total captured Post-II | Post-II survivor composition (%) |
|---|---|---|---|---|---|---|---|
| *Xenops minutus*[FI] | 3 | 1(33) | 0(0) | 3 | 33 | 0 | |
| *Dendrocincla anabatina*[FI] | 12 | 6(50) | 2(17) | 9 | 67 | 6 | 33 |
| *Dendrocincla homochroa*[FI,3] | 6 | | | 0 | | 0 | |
| *Xiphorhynchus flavigaster*[FI] | 11 | 2(18) | 1(9) | 8 | 25 | 3 | 33 |
| *Taraba major*[SI] | 4 | 1(25) | 0(0) | 3 | 33 | 5 | 0 |
| *Thamnophilus doliatus*[SI] | 6 | 5(83) | 1(17) | 7 | 71 | 7 | 14 |
| *Cercomacra tyrannina*[FI] | 22 | 4(18) | 0(0) | 13 | 31 | 6 | 0 |
| *Gymnocichla nudiceps*[FI] | 12 | 3(25) | 0(0) | 4 | 75 | 0 | |
| *Formicarius analis*[FI] | 8 | 1(13) | 1(13) | 5 | 20 | 3 | 33 |
| *Myiopagis viridicata*[FI] | 7 | 3(43) | 0(0) | 7 | 43 | 9 | 0 |
| *Mionectes oleagineus*[FF] | 121 | 9(7) | 0(0) | 64 | 14 | 5 | 0 |
| *Todirostrum sylvia*[FI] | 9 | 1(11) | 1(11) | 2 | 50 | 5 | 20 |

Appendix 1.0. (continued)

| Species | Total banded Pre-Iris | Recaptured Post-I (%) | Recaptured Post-II (%) | Total captured Post-I | Post-I survivor composition (%) | Total captured Post-II | Post-II survivor composition (%) |
|---|---|---|---|---|---|---|---|
| *Tolmomyias sulfurescens*[FI] | 6 | 2(33) | 2(33) | 12 | 17 | 6 | 33 |
| *Onychorhynchus mexicanus*[FI,3] | 5 | | | 0 | | 0 | |
| *Myiobius sulfureipygius*[FI] | 1 | 0(0) | 0(0) | 6 | 0 | 1 | 0 |
| *Attila spadiceus*[FI] | 6 | 0(0) | 0(0) | 5 | 0 | 3 | 0 |
| *Myiozetetes similis*[SO] | 3 | 0(0) | 0(0) | 0 | | 0 | |
| *Pachyramphus polychopterus*[FI] | 8 | 0(0) | 1(13) | 1 | 0 | 4 | 25 |
| *Schiffornis turdinus*[FI,3] | 5 | | | 0 | | 0 | |
| *Manacus candei*[FF] | 93 | 18(19) | 4(4) | 49 | 37 | 17 | 24 |
| *Hylophilus ochraceiceps*[FI,3] | 5 | | | 3 | | 0 | |
| *Pipra mentalis*[FF] | 7 | 0(0) | 0(0) | 27 | 0 | 1 | 0 |
| *Thryothorus maculipectus*[FI] | 25 | 7(28) | 4(16) | 11 | 64 | 14 | 29 |

Appendix 1.0. (continued)

| Species | Total banded Pre-Iris | Recaptured Post-I (%) | Recaptured Post-II (%) | Total captured Post-I | Post-I survivor composition (%) | Total captured Post-II | Post-II survivor composition (%) |
|---|---|---|---|---|---|---|---|
| *Henicorhina leucosticta*[FI] | 6 | 0(0) | 0(0) | 0 | | 0 | |
| *Ramphocaenus melanurus*[FI] | 10 | 3(30) | 2(20) | 7 | 43 | 12 | 17 |
| *Turdus grayi*[FO] | 26 | 0(0) | 0(0) | 29 | 0 | 10 | 0 |
| *Coereba flaveola*[FN] | 4 | 1(25) | 0(0) | 20 | 5 | 8 | 0 |
| *Eucometis penicillata*[FI] | 14 | 0(0) | 0(0) | 1 | 0 | 2 | 0 |
| *Habia fuscicauda*[FO] | 7 | 3(43) | 2(29) | 12 | 25 | 5 | 40 |
| *Ramphocelus sanguinolentus*[FO] | 1 | 1(100) | 0(0) | 3 | 33 | 4 | 0 |
| *Ramphocelus passerinii*[FO] | 30 | 15(50) | 0(0) | 41 | 37 | 15 | 0 |
| *Euphonia gouldi*[FO] | 4 | 1(25) | 0(0) | 5 | 20 | 0 | |
| *Volatinia jacarina*[OG] | 8 | 0(0) | 0(0) | 17 | 0 | 22 | 0 |
| *Sporophila aurita*[OG] | 141 | 10(7) | 11(8) | 114 | 9 | 101 | 11 |

Appendix 1.0. (continued)

| Species | Total banded Pre-Iris | Recaptured Post-I (%) | Recaptured Post-II (%) | Total captured Post-I | Post-I survivor composition (%) | Total captured Post-II | Post-II survivor composition (%) |
|---|---|---|---|---|---|---|---|
| *Sporophila torqueola*[OG] | 23 | 4(17) | 3(13) | 218 | 2 | 144 | 2 |
| *Oryzoborus funereus*[OG] | 34 | 2(6) | 7(21) | 35 | 6 | 27 | 26 |
| *Arremon aurantiirostris*[FO] | 6 | 2(33) | 0(0) | 3 | 67 | 0 | |
| *Arremonops chloronotus*[FO] | 13 | 1(8) | 2(15) | 3 | 33 | 8 | 25 |
| *Saltator coerulescens*[SO] | 4 | 1(25) | 0(0) | 2 | 50 | 3 | 0 |
| *Saltator maximus*[FO] | 15 | 3(20) | 1(7) | 3 | 100 | 10 | 10 |
| *Saltator atriceps*[FO] | 5 | 0(0) | 0(0) | 0 | | 1 | 0 |
| *Cyanocompsa cyanoides*[FO] | 1 | 0(0) | 0(0) | 2 | 0 | 2 | 0 |
| *Amblycercus holosericeus*[FI] | 12 | 2(17) | 0(0) | 3 | 67 | 6 | 0 |

[1]Habitat preference abbreviations: F: Forest; S: Scrub; O: Open-habitat.

Appendix 1.0. (continued)

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[2]Guild abbreviations: I: Insectivore; F: Frugivore; O: Omnivore; P: Piscivore; N: Nectarivore; G: Granivore.

[3]Some or all individuals in some species were not individually banded, so I was unable to examine site fidelity; numbers given are total captures in each period.

Chapter 2: Autumn stopover near the Gulf of Honduras by Nearctic-Neotropic migrants

## 2.1 Abstract

The southeastern Yucatan Peninsula hosts high numbers of transient Nearctic-Neotropic migrants during autumn migration, but the importance of this region during migratory stopover has not been addressed despite its proximity to the Gulf of Honduras, a potential ecological barrier to continued migration. I studied autumn fattening in tropical lowland forest 20 km inland from this gulf. Of 15 species or species complexes (hereafter 'species') with sufficient sample sizes, 10 showed significant positive diel (24 h) gains in a body condition index. Estimates of net mass gains in these 10 species suggest that they all were depositing fat, and four of those species were depositing enough fat to fuel an entire night of migration after only one day of fattening. Two of the four species apparently not gaining mass at the study site migrate late in the season and only occurred after Hurricane Iris severely altered the habitat. However, four other species showed significant gains in mass after the hurricane. Comparison of these data with other studies of fattening during autumn migration reveals regional interspecific differences in fattening strategies.

## 2.2 Introduction

The geography of North America causes Nearctic-Neotropic migrants that breed across thousands of square kilometers of boreal and temperate forest to funnel into a small fraction of the land area in the forests of Central America during the nonbreeding season. This concentration of migrants makes Central American forests vital as both wintering and stopover habitat. Migrants that pass through the Yucatan Peninsula *en route* to

wintering grounds farther south and east encounter the Gulf of Honduras, a potential ecological barrier that would require sufficient energy reserves to cross. Monroe (1968) documented a large spring migration northward across the Gulf of Honduras and speculated that a large autumn migration also occurs. With winter ranges of many migrant species extending far beyond the Gulf of Honduras (AOU 1998) and published accounts of high volumes of transient Nearctic-Neotropic migrants farther south in Panama (Galindo et al. 1963, Galindo and Mendez 1965), the forests adjacent to the Gulf of Honduras are likely to be important stopover habitat. However, there is no information about how transient migrants use stopover sites in this region.

Further, few studies have addressed energetic needs of migrants in Central America (e.g., Rogers and Odum 1966, Child 1969, Winker 1995a,b), and there are no studies of fattening by migrants preparing to cross the Gulf of Honduras. I chose a site near the Gulf of Honduras in lowland tropical forest to examine the autumn migration of Nearctic-Neotropic migrants. I provide the first extensive data on autumn stopover by woodland migrants in this region to address the following questions: What levels of fat are carried in the region? Do migrants fatten at this site, and if so, to what extent? Do species that have farther to migrate fatten more? Given the data from this site in the context of similar studies, are there broad geographic trends to autumn fattening among North American passerine migrants?

## 2.3 Methods

### *2.3.1 Field methods*

My study site was 25-year-old second-growth lowland forest adjacent to a citrus orchard in the floodplain of the Rio Grande (16° 15.82' N, 88° 52.37' W) near Big Falls Village, Toledo District, Belize (Fig. 2.1). The site was situated in a matrix of human-altered habitats (primary forest remnants, citrus orchard, fields, and various stages of re-growth), and had a canopy height of approximately 20 m, with some gaps filled with dense woody vegetation and viny tangles of 3 m in height. In August 2001 I established a 1.26 ha study site of 30 mist nets spaced 30 m apart. Nets 12 m long were placed in two rows of 15, with mesh sizes alternating between 30 and 36 mm. Nets were opened beginning on 11 August (all day long when conditions permitted). I accrued 8,805 net hours until 7 October, when nets were removed from the study site in anticipation of Hurricane Iris, which struck on 8 October. The effect of Hurricane Iris on the site was to change the habitat from a nearly closed canopy 20 m high to a 5 m high tangle of uprooted and broken trees, broken branches, and vines. On 19 October I re-opened 15 nets placed on the original site in one row along its long axis. Five nets were placed back in their original net lanes, but placement of nets was constrained by the drastically altered forest structure (e.g., fallen trees and dense tangles of vines). During this period, I only netted during the mornings and evenings due to the lack of shade on the plot. I accrued 1,114 more net hours and concluded the effort on 15 November.

Each bird captured was identified to species, then aged and sexed if possible. Time and net of capture, mass, and wing chord were recorded for all captures; tail, tarsus, and bill lengths were recorded for most individuals. Subcutaneous fat deposits were scored according to Helms and Drury (1960). The genus *Empidonax* was treated as a

single taxon because of the difficulty of separating the 5 Nearctic-Neotropic migrant species present (*traillii*, *alnorum*, *flaviventris*, *virescens*, and *minimus*). The morphological measurement and mass data for this genus were normally distributed.

*2.3.2 Data analyses:*

*2.3.2.1 Daily mass gains*

The extent of fat deposition was estimated at the species level following the methodology of Winker et al. (1992a) and Winker (1995a), and is based on the following logic: At any given stopover site, few banded individuals are recaptured within a season, and those individuals may not be representative of the non-recaptured individuals, and are often leaner than the species average on initial capture (Winker et al. 1992a). In analyses of mass changes in recaptured individuals at other stopover sites, recaptured individuals often lost mass (e.g., Rogers and Odum 1966, Rappole and Warner 1976, Winker et al. 1992a, Yong and Moore 1997), and this may be due to handling effects (Odum 1960, Rogers and Odum 1966). I excluded recaptures from these analyses to control for possible handling effects. Transient nocturnal migrants present during the day at a stopover site that has sufficient resources should be accumulating energy stores (mostly fat) to fuel the next bout of migration, and, at the species level, regression of body mass on time of day should reveal a positive relationship. Among migrant birds, mass is influenced by overall body size and fat loads (e.g., Child 1969), and mass gains due to the accumulation of fat may be masked by the variability of body size in a species. Mass is a reasonable predictor of a migrant's fat content when it is standardized for body size (Odum 1960, Connell et al. 1960, Rogers and Odum 1964, 1966). If the mass of

captured individuals is standardized for body size, there will be a greater likelihood of detecting a species-level trend in mass gain due to increased energy stores.

What is a good measure of body size? Rising and Sommers (1989) and Freeman and Jackson (1990) both suggested that no single linear external measurement of a bird is a good correlate of body size, although these studies suggested that tarsometatarsus ("tarsus") or tibiotarsus were the best univariate indicators of body size. However, Connell et al. (1960) and Rogers and Odum (1964, 1966) showed that wing length is a good predictor of fat-free mass in some species of passerines, and, although these authors did not examine other variables, Winker (1995a) also found wing chord or tail to be better predictors of fat content than tarsus in a sample of Tennessee Warblers (*Vermivora peregrina*). I used wing chord to standardize the mass by calculating a condition index (see following) for all species but Kentucky Warbler in this study (see Results).

A condition index for each individual was calculated by dividing its mass by its wing chord (Winker 1995a). For each species, condition index was examined with respect to time of day (equivalent to time of capture of each individual; hereafter referred to simply as 'time') using simple linear regression. Regressions of fat scores, mass, and condition indices using other morphological characters (tail, tarsus, and bill length) with respect to time were used to corroborate wing chord condition index trends.

In species having slopes of regressions of condition index with respect to time significantly different from zero ($\alpha = 0.05$), estimates of net 24 hour mass changes were estimated. The slope of the condition index regressions were converted to estimated daily gross mass gains in a species by multiplying by 12.4 h (average length of daily bird

activity from field notes) and then multiplying by the sample's mean wing chord. Net mass gains were calculated by subtracting estimates of nightly metabolic demands from the gross daily gains. One estimate of nocturnal loss was 4.5% of mean body mass, which was the average daily mass variation given by Baldwin and Kendeigh (1938), and for another, more conservative estimate, I used 4.5% of mean body mass plus estimated overnight mass loss calculated from standard metabolic estimates using equation (e) in Lasiewski and Dawson (1967), which was based on 35 species of passerines.

Fat is the main energy source during avian migration, making fat deposition critical to migratory birds, and, although most energetic needs in migration are supplied by fat deposits (Dawson et al. 1983, Blem 1990), there is evidence that other tissues also contribute to a migrant's energetic demands (e.g., Rogers and Odum 1966, Karasov and Pinshow 1998, Piersma 1998, Bauchinger and Biebach 2000, Klaassen et al. 2000, Gannes 2002). Fat gains are highly correlated with mass gains (e.g., Klaassen et al. 2000), and although "fattening" is used in this paper to refer to the accumulation of energy stores, which are inferred from mass gains, this does not imply that all mass gained is fuel, nor that all fuel gained is fat, although for flight distance estimates the assumption is made that all mass gained is fat.

Morphological data for each species were checked for normality. Wing chord in American Redstarts was not normally distributed and various transformations failed to normalize these data. Besides American Redstart wing chord, mass and morphological variables used to estimate net mass gains in each species were normally distributed. Following regression analyses, residuals were checked for normality using quantile-

quantile plots, and examined visually to see if there were any patterns that indicated unequal variance. Residuals were normal, and no patterns indicating heteroscedasticity were found in any species.

Hurricane Iris struck on 8 October 2001. This drastic change in habitat appeared to change energetic dynamics among resident species. This change may also have had an effect on fat deposition by migrants in the hurricane-altered habitat. No migrant species had large enough sample sizes ($N \geq 30$) pre- and post-hurricane to conduct separate analyses both before and after the storm. Given the changes observed in the resident community after Hurricane Iris, each migrant species considered here was based on a sample from either entirely before or entirely after the hurricane only; samples were not pooled between pre- and post-hurricane efforts (Table 2.1).

*2.3.2.2 Flight distance estimates*

The maximum flight distance possible for each species' average gain at the site was estimated by using net gain estimates from this study, published values for the energetic content of fat (39.8 kJ/g; Nisbet et al. 1963), and rate of energy use during migration (Tucker 1974). These flight distance estimates were used to estimate how far an average individual of each species might travel in still air given estimated net mass gains and flight range estimates from Tucker (1974). Changes in mass due to changes in water content are assumed to be negligible (Nisbet et al. 1963).

*2.3.2.3 Mass comparisons*

Condition index analyses provide an estimate of the extent of the gains in mass, but do not consider the amount of fat already carried by the species. To examine the fat

load each species was carrying, average mass from each species was compared to the average fat-free mass for the species (Odum *in* Dunning 1993) using one-sample *t*-tests. I also compared mean species mass and morphology (wing chord and tail length) between my site and Veracruz, Mexico (Winker 1995a) using *t*-tests to see if there were differences in mass that may have been due to changes in fat content.

**2.4 Results**

I captured 30 or more individuals of 14 species and the genus *Empidonax*, and summary statistics of morphological characters are presented to allow comparisons with other studies (Table 2.1). As Winker (1995), I found that actively growing feathers were rare, and assume that energetic demands for these birds were limited to migration and maintenance costs.

*2.4.1 Comparisons of mass with fat-free mass*

All species but the Wood Thrush were significantly heavier than the species' average fat-free mass (Odum *in* Dunning 1993; Table 2.2), and most individuals were carrying visible subcutaneous fat (82% of the 15 Nearctic-Neotropic migrants considered here had fat scores > 0). Many individuals of Veery and Swainson's Thrush carried heavy fat loads (Table 2.1; all Veeries had fat scores > 0). Although this study did not include dietary analysis, frequent defecation of birds during handling suggested they were feeding at the site, and the peak migration, especially of *Catharus* thrushes, corresponded to the ripening of large numbers of fruits on the plot, particularly *Dendropanax arboreus* (Araliaceae).

*2.4.2 Estimates of daily mass gain*

Eleven species had significant slopes of mass with respect to time (Table 2.3). Wing chord condition index regressions with respect to time with significant *F*-values (slopes different from zero); all were positive for nine species (Table 2.3). Kentucky Warblers and Veeries did not show significant gains in wing chord condition index, even though regressions of mass on time had significantly positive slopes, and fat score regressions with respect to time also showed significant positive slopes in Kentucky Warblers. Both species had marginal *P*-values for gain in wing chord condition index with respect to time (Kentucky Warbler $P = 0.064$, Veery $P = 0.068$; Table 2.3).

Four species had significantly positive slopes of fat scores with respect to time (Table 2.3), and all of these species also had significant slopes of mass with respect to time. Of these four, only the Kentucky Warbler did not also have a significant slope in wing chord condition index with respect to time (Table 2.3). Because this species had significant slopes of mass and fat score with respect to time (Table 2.3), it appeared that Kentucky Warblers were fattening at the site, even though wing chord regression with respect to time was not significant. I used tail condition index, which had a slope significantly different from zero (Table 2.3), to obtain an estimate of net daily mass gain in this species.

In Swainson's Thrushes and Red-eyed Vireos, regressions of wing chord with respect to time revealed a significant positive slope (Table 2.3), suggesting that larger individuals of these two species were more likely to be captured later in the day.

Linear models (Table 2.4) for the 10 species that had significant slopes of condition index with respect to time (Table 2.3) were used to estimate gross daily mass gains (Table 2.5). From these gross mass gains, net mass gains were calculated by subtracting estimates of nocturnal losses due to metabolism, and these net gains were the basis for flight range estimates (Table 2.5).

*2.4.3 Flight distance estimates*

The distance from the study site to the nearest land on the opposite side of the Gulf of Honduras (Cabo de Tres Puntas, Guatemala) is about 43 km, and, among the 10 species showing gains, at least one estimate in all species but Swainson's Thrush showed that the average individual was gaining energetic reserves at a rate sufficient to fly this distance (Table 2.5). Flight range estimate 1 for Indigo Bunting was also less than 43 km (Table 2.5). In four species (*Empidonax*, Gray catbird, Red-eyed Vireo, and Northern Waterthrush), the most conservative estimates showed substantial net diel mass gains (≥ 7.7% of mean body mass), suggesting that individuals of these species could fly for between eight and ten hours (over 200 km) if all mass gained was fat (Table 2.5). Maximum range estimates in these species are between ten and fourteen hours of flight (over 260 km; Table 2.5).

*2.4.4 Mass comparisons with Veracruz, Mexico*

Mass comparisons with Veracruz, Mexico, another Neotropical site, were possible (Winker 1995a). Gray Catbirds and Kentucky Warblers were significantly heavier in Belize than Veracruz (Table 2.6), but Wood Thrush, Red-eyed Vireo, Magnolia Warbler, and American Redstart were significantly lighter in Belize compared to Veracruz (Table

2.6). However, all species in Veracruz had significantly longer wing chords (Table 2.6), and all but Wood Thrush Red-eyed Vireo, and Hooded Warbler also had significantly longer tail length (Table 2.6).

**2.5 Discussion**

Ten of 15 species studied apparently used this site to acquire resources and deposit fat, and no species had significantly negative daily mass gain estimates. Just one species (Wood Thrush) had a mean mass that was not significantly higher than average fat-free mass. Fattening differences among species at this site showed that not all species fatten, and, among species that fatten, the degree of fattening varied. Comparison among sites showed geographic differences in fattening strategy within species during autumn migration.

In Swainson's Thrush and Red-eyed Vireo, the significant increasing trend in wing chord with respect to time suggests a size bias in time of capture over the course of the day (Table 2.3), and dividing mass by a character correlated with time could bias the net mass gain estimate. I examined mass gain estimates using condition indices derived from different morphological characters (tail, tarsus, and bill lengths) and found that choice of condition index can affect the mass gain estimate, and not all condition index regressions with respect to time had slopes significantly different from zero. The slope of the regression of mass with respect to time was significantly positive in both species, and the slope of fat score with respect to time was also significantly positive in Swainson's Thrush (Table 2.3). Given that regressions of other condition indices and mass with respect to time were significant in both species, and that fat score regressions with respect

to time were significant in Swainson's Thrush, it is likely that these two species were fattening at the site. The estimates from wing chord condition index had the most conservative mass gains and were used as the basis for further analyses in both species.

Only four species (*Empidonax,* Swainson's Thrush, Kentucky Warbler, and American Redstart) showed significant gains in fat scores with respect to time (Table 2.3). All of these species showed significant mass gains with respect to time, and all but Kentucky Warbler showed significant wing chord condition index increases with respect to time (Kentucky Warbler had a significant tail condition index; Table 2.3). Ideally, significant condition index trends would be corroborated by significant fat score regressions. However, in these data, only 40% of species with significant mass gain estimates also had significant fat score trends. Fat scores are subjective ordinal estimates of the fat content in birds, not absolute measures, and they score only visible subcutaneous deposits on the venter of a bird, even though fat is also deposited in other areas (King and Farner 1965). Rogers (1991) showed in wintering Dark-eyed Juncos (*Junco hyemalis*) that the association between lipid index (g lipid/g lean dry mass) from fat extractions and fat scores taken by one experienced observer on the same birds was high ($R^2 = 0.974$). With an experienced observer, he showed that fat scores were able to detect small changes in fat stores, but cautioned that inter-observer differences in fat scores could affect analyses of fat score data. Fat scores were taken by two observers during my study, and one had never used the technique before. It is likely that the lack of significance in fat score regressions when so many species showed significant mass and condition index gains was, at least in part, due to inter-observer variation, and the

confounding factor of observer inexperience. Therefore, I proceed cautiously, emphasize that these are estimates, but assume that gains in condition index reflect gains in mass due to fattening.

I assume mass gain is not due to recuperation of water lost due to dehydration during migration (Nisbet et al. 1963). Catabolism of lipids produces water that helps to maintain water balance, and Rogers and Odum (1966) showed that even in emaciated post-flight birds in Panama, water content was not different from fat birds. Bauchinger and Biebach (2000) also showed that water content did not differ among pre-migratory, immediately post-migratory, or post-migratory birds that had 7 days to recover with free access to food and water.

These data suggest that at least 10 of 15 species fatten at this site from daily net mass gain estimates (Table 2.5). Two of the five species apparently not fattening, Wood Thrush and Common Yellowthroat, were sampled only in the post-hurricane effort. However, four other species sampled only in the post-hurricane effort (Gray Catbird, Magnolia Warbler, American Redstart and Indigo Bunting) showed significant positive slopes of wing chord condition index with respect to time (Table 2.3).

Five of 15 species apparently were not depositing fat. There is no apparent reason why five were not depositing fat when the rest were. Habitat degradation by Hurricane Iris may be responsible for why Wood Thrushes and Common Yellowthroats did not deposit fat, even though other species were depositing fat in the same post-hurricane habitat. Why Veeries, Hooded Warblers and Ovenbirds did not deposit fat during the pre-hurricane period is not apparent either.

The substantial net gain estimates in some species (Empidonax, Red-eyed Vireo, Gray Catbird, and Northern Waterthrush) suggest that the habitat at this site was favorable enough to allow for a full night of migration after spending only one day fattening (Table 2.5). Based on estimates of flight distances (Table 2.5), the Gulf of Honduras is an ecological barrier that migrants continuing from southern Belize farther into Central America are able to overcome, and it appears that most migrants departing from this site could travel over 100 km if all mass gain was fat (Table 2.5).

These data cannot address year-to-year variability in fattening at this site. However, in Minnesota during a three-year study, species with significant daily gains in one year often showed significant gains in more than one year (Winker 1995a). Prior to the arrival of Hurricane Iris, migrants at the Belize site were probably using this site consistently from one year to the next. However, habitat damage wrought by the hurricane may have changed the suitability of the site for fattening by some of the migrants, particularly those six species considered here for which all of the sample came from the post-hurricane period. For those species, my results may not be typical for the region.

*2.5.1 Geographic trends in fattening*

Fattening trends were available from three other mainland sites in North America (Table 2.7): The St. Croix River valley, Minnesota (Winker et al. 1992a, b), the Sierra de los Tuxtlas, Veracruz (Winker 1995a), and the north shore of Lake Erie, Ontario (Dunn 2001). The data of Morris et al. (1996) on Appledore Island, Maine are excluded because

most stopover habitat is not on islands near ecological barriers, and the individuals present there may not be representative of the species stopping over in the region.

Fattening data for most species are sparse across their migration routes, but some patterns are apparent (Table 2.7). Many species (Swainson's Thrush, Magnolia Warbler, American Redstart, Northern Waterthrush, and Wilson's Warbler) appear to fatten repeatedly all along their migration routes despite the energetic demands of molt at higher latitudes (Winker et al. 1992a, b). At higher latitudes, Red-eyed Vireos apparently do not accumulate large amounts of fat, and Gray Catbirds apparently lose mass in Minnesota, but Red-eyed Vireos showed fattening trends from near the northern coast of the Gulf of Mexico, and both species appear to fatten in the tropics (Table 2.7). This may be because completing prebasic molt in these species at higher latitudes takes priority over fattening (Winker et al. 1992a). Ovenbirds and Hooded Warblers did not show fattening trends in the tropics, although Ovenbirds did fatten at Lake Erie (Table 2.7). No data are available for Hooded Warblers in the southern United States. Worm-eating and Kentucky Warblers also lack data from the southern United States, but both appear to fatten in the tropics.

It is clear that not all species have adopted the same strategy along their autumn migration routes. Some species (Red-eyed Vireo) only show signs of significant fattening in the tropics (Table 2.7). Other species (Magnolia Warbler, American Redstart, Northern Waterthrush, and Wilson's Warbler) show consistent mass gains from all stopover sites studied (Table 2.7). Ovenbirds demonstrate significant fattening at

northern stopover sites, but apparently do not deposit significant amounts of fat once they reach tropical latitudes (Table 2.7).

Differences in body mass from Veracruz suggest that some species carried different fat loads at different sites (Table 2.6). However, morphological comparisons between Belize and Veracruz showed significant differences (Table 2.6), and given that wing chord and tail length are correlated with body size, the differences in mass between these study sites may be due to differences in body size rather than fat loads. It is likely that Kentucky Warblers and Gray Catbirds were fatter in Belize than Veracruz, because their mass was significantly greater in Belize despite their apparent smaller body size (significantly shorter wing chord and tail length; Table 2.6) in Belize. Many species examined were consistent in their differences (Veracruz birds generally were larger and had greater mass); however, the variability in the differences among species suggests inter-observer variation was not the cause of these differences (i.e., if the differences were due to inter-observer variation, some proportional consistency in the differences between the sites would be expected). The size differences between these two sites may be due to different migration routes among different populations.

Why weren't all species fattening in Belize? Species such as Veery and Swainson's Thrush, whose winter ranges are entirely or largely in South America were predicted to have been fattening as much as Red-eyed Vireos, which also winter entirely in South America. Winker (1995a) suggested that some species on the Isthmus of Tehuantepec may not have been fattening because a higher proportion of migrants may have been close to their destinations, and a higher degree of resource certainty in the

tropics compared to temperate habitats would not require depositing large amounts of fat. It is important to note that in this Belize study the Wood Thrush was the only species not significantly heavier than the average fat-free mass (Table 2.2), and some species were already carrying heavy fat loads (Table 2.1). This may explain why Veeries apparently were not fattening at the site (Table 2.3), and Swainson's Thrushes had the lowest estimate of all fattening species (Table 2.5). The significant difference between fat-free mass and mean mass at my site and heavy fat loads in several species suggest that stopover sites farther north are important areas for fattening.

Ten Nearctic-Neotropic migrant species showed evidence of fattening at my site, and this study suggests that lowland forests in the southeastern Yucatan Peninsula are important to many species of transient migrants as an area build fuel stores. Some species deposit enough fat in one day to fuel an entire night of migration the next night. However, some species apparently fatten farther north and arrive at this site already carrying high fat loads. Only one species (Wood Thrush) was not significantly heavier than its average fat-free mass. Combined with other studies of fattening and stopover ecology of North American Nearctic-Neotropic migrants, this study is helpful for beginning to develop hypotheses about geographic variation and interspecific differences in fat deposition strategies. Much work remains to be done in many of these same areas during spring migration, and there are no data during any season from South America, Central America between Belize and Panama, or the southeastern United States. However, apparently more than one strategy for fattening has evolved among these passerine migrants in northern Central America.

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Table 2.1. Mean measures of morphological characters ± standard deviation and sample sizes of autumn migrants from Big Falls, Belize.

| Species | Mass | (*N*) | Wing chord | (*N*) | Tail length | (*N*) | Tarsus length | (*N*) | Bill length | (*N*) | Fat Mean | (*N*) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Empidonax* spp. | 11.73± 1.39 | (88) | 65.88± 3.14 | (88) | 54.19± 2.93 | (86) | 15.52± 0.98 | (88) | 8.87± 0.58 | (88) | 0.7 | (79) |
| Red-eyed Vireo *Vireo olivaceus* | 16.88± 1.50 | (39) | 74.92± 2.35 | (39) | 50.44± 2.97 | (39) | 17.67± 1.32 | (39) | 9.65± 0.41 | (39) | 1.3 | (39) |
| Veery *Catharus fuscescens* | 32.15± 4.29 | (67) | 92.70± 3.05 | (67) | 66.51± 3.75 | (67) | 28.85± 1.46 | (67) | 9.63± 0.49 | (67) | 1.7 | (67) |
| Swainson's Thrush *Catharus ustulatus* | 29.36± 3.13 | (305) | 93.22± 2.90 | (305) | 64.05± 3.25 | (305) | 26.99± 1.39 | (305) | 8.93± 0.46 | (305) | 1.7 | (305) |
| Wood Thrush[1] *Hylocichla mustelina* | 42.93± 3.17 | (45) | 101.36± 3.69 | (45) | 68.00± 2.54 | (19) | 30.01± 0.99 | (19) | 11.47± 0.47 | (19) | 0.7 | (42) |
| Gray Catbird[1] *Dumetella carolinensis* | 34.35± 2.88 | (268) | 85.53± 2.44 | (269) | 88.02± 4.29 | (117) | | | 11.20± 0.47 | (120) | 1.4 | (265) |

Table 2.1. (continued)

| Species | Mass | (*N*) | Wing chord | (*N*) | Tail length | (*N*) | Tarsus length | (*N*) | Bill length | (*N*) | Fat Mean | (*N*) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Magnolia Warbler[1] | 7.17± 0.47 | (78) | 56.46± 2.26 | (77) | 47.70± 2.19 | (76) | 17.24± 0.93 | (5) | 7.03± 0.36 | (66) | 0.6 | (79) |
| *Dendroica magnolia* | | | | | | | | | | | | |
| American Redstart[1] | 6.93± 0.50 | (34) | 57.71± 1.84 | (31) | 53.71± 2.13 | (28) | 16.76± 0.59 | (27) | | | 0.4 | (34) |
| *Setophaga ruticilla* | | | | | | | | | | | | |
| Worm-eating Warbler | 12.27± 0.80 | (31) | 64.85± 1.86 | (31) | 46.76± 2.22 | (31) | 17.83± 0.50 | (31) | 10.59± 0.49 | (31) | 0.7 | (29) |
| *Helmitheros vermivorus* | | | | | | | | | | | | |
| Ovenbird | 17.44± 1.25 | (44) | 70.28± 2.69 | (43) | 50.88± 2.50 | (42) | 21.54± 0.93 | (43) | 8.75± 0.45 | (43) | 0.7 | (44) |
| *Seiurus aurocapillus* | | | | | | | | | | | | |
| Northern Waterthrush | 15.53± 1.41 | (85) | 71.22± 2.15 | (84) | 49.28± 2.55 | (84) | 21.08± 0.53 | (84) | 9.69± 0.45 | (84) | 1.0 | (86) |
| *Seiurus noveboracensis* | | | | | | | | | | | | |
| Kentucky Warbler | 12.77± 1.11 | (60) | 63.59± 2.55 | (59) | 45.88± 2.62 | (59) | 21.56± 0.73 | (59) | 8.40± 0.33 | (59) | 1.0 | (56) |
| *Oporornis formosus* | | | | | | | | | | | | |

Table 2.1. (continued)

| Species | Mass | (*N*) | Wing chord | (*N*) | Tail length | (*N*) | Tarsus length | (*N*) | Bill length | (*N*) | Fat Mean | (*N*) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Common Yellowthroat[1] *Geothlypis trichas* | 9.31± 0.69 | (47) | 51.99± 2.42 | (48) | 48.50± 2.62 | (31) | 19.61± 0.62 | (29) | 7.94± 0.40 | (28) | 0.9 | (47) |
| Hooded Warbler *Wilsonia citrina* | 9.41± 0.62 | (50) | 61.55± 2.22 | (51) | 54.64± 1.80 | (50) | 19.12± 0.62 | (49) | 7.89± 0.35 | (49) | 0.4 | (49) |
| Indigo Bunting[1] *Passerina cyanea* | 13.50± 1.06 | (88) | 62.40± 2.50 | (87) | 49.33± 2.33 | (65) | 16.85± 0.54 | (83) | 7.90± 0.39 | (63) | 0.9 | (84) |

[1]Sample is entirely from after Hurricane Iris struck (8 October 2001).

Table 2.2. Comparison of masses in Belize to fat-free masses (Odum in Dunning 1993).

| | | Fat-free mass | Belize mass | *t* |
|---|---|---|---|---|
| Red-eyed Vireo | mean | 14.59 | 16.88 | 10.14** |
| | sd | 1.31 | 1.50 | |
| | N | 323 | 39 | |
| Veery | mean | 26.66 | 32.15 | 8.92** |
| | sd | 3.61 | 4.29 | |
| | N | 100 | 67 | |
| Swainson's Thrush | mean | 24.18 | 29.36 | 23.50** |
| | sd | 2.2 | 3.13 | |
| | N | 299 | 305 | |
| Wood Thrush | mean | 42.21 | 42.93 | 1.23 |
| | sd | 3.32 | 3.17 | |
| | N | 105 | 45 | |
| Gray Catbird | mean | 31.8 | 34.35 | 8.17** |
| | sd | 2.13 | 2.89 | |
| | N | 104 | 268 | |
| Magnolia Warbler | mean | 6.92 | 7.17 | 2.63* |
| | sd | 0.49 | 0.47 | |
| | N | 35 | 78 | |

Table 2.2. (continued)

| | | Fat-free mass | Belize mass | *t* |
|---|---|---|---|---|
| American Redstart | mean | 6.49 | 6.93 | 5.03** |
| | sd | 0.42 | 0.50 | |
| | N | 102 | 34 | |
| Worm-eating Warbler | mean | 10.79 | 12.27 | 7.17** |
| | sd | 0.78 | 0.80 | |
| | N | 28 | 31 | |
| Ovenbird | mean | 15.52 | 17.44 | 7.54** |
| | sd | 0.87 | 1.25 | |
| | N | 33 | 44 | |
| Northern Waterthrush | mean | 13.68 | 15.53 | 9.02** |
| | sd | 1.3 | 1.41 | |
| | N | 89 | 85 | |
| Kentucky Warbler | mean | 11.36 | 12.77 | 9.25** |
| | sd | 0.96 | 1.11 | |
| | N | 156 | 60 | |
| Common Yellowthroat | mean | 8.36 | 9.31 | 5.38** |
| | sd | 0.54 | 0.69 | |
| | N | 19 | 47 | |

Table 2.2. (continued)

| | | Fat-free mass | Belize mass | *t* |
|---|---|---|---|---|
| Hooded Warbler | mean | 8.2 | 9.41 | 9.37** |
| | sd | 0.84 | 0.62 | |
| | N | 153 | 50 | |
| Indigo Bunting | mean | 12.34 | 13.50 | 8.76** |
| | sd | 0.95 | 1.06 | |
| | N | 155 | 88 | |

* $P < 0.005$; ** $P < 0.0005$.

Table 2.3. Relationships between morphological characters of individuals and time of capture.[1]

| | Mensural characters[2] | | | | Condition indices | |
|---|---|---|---|---|---|---|
| Species | Wch | Tl | Mass | Fat | Wch | Tl |
| *Empidonax* | 0.21 | 3.13 | 8.77* | 7.72* | 9.80* | 4.76* |
| Red-eyed Vireo | 5.30* | 2.28 | 8.31* | 0.48 | 4.09* | 2.99 |
| Veery | 1.91 | 1.21 | 4.76* | 2.98 | 3.46 | 2.80 |
| Swainson's Thrush | 8.52* | 4.02* | 7.87* | 13.12* | 4.18* | 3.17 |
| Wood Thrush | 0.18 | 0.16 | 0.07 | 2.79 | 0.23 | |
| Gray Catbird | 2.20 | 0.24 | 24.21* | 0.64 | 18.83* | 4.99* |
| Magnolia Warbler | 0.37 | 0.39 | 6.54* | 3.40 | 7.00* | 8.72* |
| American Redstart | 2.18[3] | | 6.74* | 6.60* | 6.56* | |
| Worm-eating Warbler | 1.07 | 1.09 | 8.64* | 1.17 | 6.50* | 3.97 |
| Ovenbird | 0.02 | 0.02 | 2.06 | 1.96 | 2.91 | 1.65 |
| Northern Waterthrush | 0.09 | 1.78 | 8.15* | 2.80 | 8.75* | 3.14 |
| Kentucky Warbler | 3.85 | 0.46 | 7.41* | 4.41* | 3.57 | 5.24* |
| Common Yellowthroat | 0.20 | 0.02 | 0.77 | 0.42 | 0.48 | 1.75 |
| Hooded Warbler | 0.01 | 0.16 | 1.77 | 0.16 | 2.29 | 1.36 |
| Indigo Bunting | 0.02 | 0.92 | 4.34* | 0.14 | 5.03* | 0.88 |

[1]Values are F-statistics from linear regressions, and test the null hypothesis that the slope of the linear model is not significantly different from zero.

Table 2.3. (continued)

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[2]Wch = Wing chord; Tl = Tail length.

[3]Variable not normally distributed.

* $P < 0.05$.

Table 2.4. Summary of linear models for diurnal change in condition index for species in Table 2.3 for which gains can be estimated.[1]

| Species | *N* | *b* | *m* | SE *m* | *F* | *P* | $R^2$ | Condition gain/day[2] |
|---|---|---|---|---|---|---|---|---|
| *Empidonax* | 88 | 0.14936 | 0.00260 | 0.00083 | 9.80 | 0.0025 | 0.11 | 0.03228 |
| Swainson's Thrush | 306 | 0.29956 | 0.00133 | 0.00065 | 4.18 | 0.0418 | 0.01 | 0.01651 |
| Gray Catbird | 269 | 0.36757 | 0.00406 | 0.00094 | 18.83 | <0.0001 | 0.07 | 0.05041 |
| Magnolia Warbler | 77 | 0.11762 | 0.00106 | 0.00040 | 7.00 | 0.0100 | 0.09 | 0.01316 |
| Red-eyed Vireo | 39 | 0.19128 | 0.00276 | 0.00136 | 4.09 | 0.0504 | 0.10 | 0.03427 |
| Worm-eating Warbler | 31 | 0.17130 | 0.00160 | 0.00063 | 6.50 | 0.0165 | 0.19 | 0.01987 |
| Kentucky Warbler[3] | 59 | 0.25142 | 0.00243 | 0.00106 | 5.24 | 0.0259 | 0.09 | 0.03017 |
| Northern Waterthrush | 84 | 0.19323 | 0.00250 | 0.00085 | 8.75 | 0.0041 | 0.10 | 0.03104 |
| American Redstart | 31 | 0.11017 | 0.00086 | 0.00034 | 6.56 | 0.0157 | 0.18 | 0.01071 |
| Indigo Bunting | 87 | 0.20401 | 0.00138 | 0.00062 | 5.03 | 0.0274 | 0.06 | 0.01714 |

Table 2.4. (continued)

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[1]Equations are $Y = b + mX$, where $Y$ is the intercept, $m$ is slope, and $X$ is time. $F$-statistic and corresponding $P$-value tell whether the slope is different from zero. $R^2$ is the coefficient of determination, and serves as a measure of the strength of the relationship between time ($X$) and condition ($Y$)

[2]Units are g/mm for the average day length of 12.42 h.

[3]Tail condition index used to estimate mass gain.

Table 2.5. Estimates of daily net increase in mass using wing chord condition index (Kentucky Warbler uses tail condition index). Units are grams, except where noted.

| Species | Gross gain/day[1] | Nocturnal loss[2] | 4.5% of mass[3] | Net gain/day[4] 1 | Net gain/day[4] 2 | Flight cost (g/h)[5] | Increase as percentage of mass 1 | Increase as percentage of mass 2 | Hours of flight[6] 1 | Hours of flight[6] 2 | Possible flight distance[7] 1 | Possible flight distance[7] 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Empidonax* | 2.13 | 0.26 | 0.53 | 1.34 | 1.60 | 0.11 | 11.43 | 13.63 | 11.96 | 14.26 | 295 | 348 |
| Red-eyed Vireo | 2.57 | 0.34 | 0.76 | 1.47 | 1.81 | 0.16 | 8.72 | 10.71 | 9.21 | 11.31 | 247 | 301 |
| Swainson's Thrush | 1.54 | 0.50 | 1.32 | -0.28 | 0.22 | 0.27 | -0.96 | 0.74 | 0 | 0.80 | 0 | 25 |
| Gray Catbird | 4.31 | 0.56 | 1.55 | 2.77 | 3.75 | 0.32 | 8.05 | 10.92 | 8.66 | 11.74 | 216 | 269 |
| Magnolia Warbler | 0.74 | 0.18 | 0.32 | 0.24 | 0.42 | 0.07 | 3.34 | 5.86 | 3.45 | 6.05 | 80 | 139 |
| American Redstart | 0.62 | 0.18 | 0.31 | 0.13 | 0.31 | 0.07 | 1.88 | 4.42 | 1.94 | 4.56 | 50 | 104 |
| Worm-eating Warbler | 1.29 | 0.27 | 0.55 | 0.47 | 0.74 | 0.12 | 3.83 | 6.00 | 4.01 | 6.29 | 103 | 160 |
| Northern Waterthrush | 2.21 | 0.32 | 0.70 | 1.20 | 1.51 | 0.15 | 7.70 | 9.74 | 8.11 | 10.26 | 215 | 269 |

Table 2.5. (continued)

| Species | Gross gain/day[1] | Nocturnal loss[2] | 4.5% of mass[3] | Net gain/day[4] 1 | Net gain/day[4] 2 | Flight cost (g/h)[5] | Increase as percentage of mass 1 | Increase as percentage of mass 2 | Hours of flight[6] 1 | Hours of flight[6] 2 | Possible flight distance[7] 1 | Possible flight distance[7] 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kentucky Warbler | 1.38 | 0.27 | 0.57 | 0.54 | 0.81 | 0.12 | 4.23 | 6.34 | 4.50 | 6.75 | 115 | 171 |
| Indigo Bunting | 1.07 | 0.29 | 0.61 | 0.18 | 0.46 | 0.13 | 1.30 | 3.42 | 1.37 | 3.59 | 36 | 94 |

[1]Mass gain during one day for average individual, using average size for wing chord (Kentucky Warbler uses tail length) from Table 1.

[2]From Lasiewski and Dawson (1967).

[3]Loss due to metabolism overnight (Baldwin and Kendeigh 1938).

[4]Net 24-h mass gain after subtraction of nightly mass loss using: (1) 4.5% of mass and standard metabolic rate; and (2) 4.5% of mass alone.

Table 2.5. (continued)

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[5]Cost of flight in grams of fat per hour, calculated after Tucker (1974:306) using average mass of captured individuals.

[6]Hours of flight possible if net gain is all fat (calculated from Tucker 1974).

[7]Kilometers of possible flight if all gain is fat (calculated from Tucker 1974).

Table 2.6. Comparisons of mass and morphological measurements between Belize and Veracruz (Winker 1995).

| | | Mass | | | Wing chord | | | Tail length | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Veracruz | Belize | *t* | Veracruz | Belize | *t* | Veracruz | Belize | *t* |
| Red-Eyed Vireo | mean | 18.55 | 16.88 | -4.51* | 76.99 | 74.92 | -5.15* | 50.85 | 50.44 | -0.90 |
| | sd | 2.24 | 1.50 | | 2.35 | 2.35 | | 2.64 | 2.97 | |
| | N | 273 | 39 | | 273 | 39 | | 273 | 39 | |
| Wood Thrush | mean | 44.25 | 42.93 | -1.94* | 102.71 | 101.36 | -1.94* | 67.53 | 68.00 | 0.61 |
| | sd | 3.63 | 3.17 | | 3.39 | 3.69 | | 3.06 | 2.54 | |
| | N | 60 | 45 | | 60 | 45 | | 60 | 19 | |
| Gray Catbird | mean | 33.81 | 34.35 | 1.65* | 88.47 | 85.53 | -10.51* | 89.36 | 88.02 | -2.49* |
| | sd | 2.72 | 2.89 | | 2.47 | 2.44 | | 3.67 | 4.29 | |
| | N | 107 | 268 | | 107 | 269 | | 107 | 117 | |
| Magnolia Warbler | mean | 7.45 | 7.17 | -3.35* | 58.54 | 56.46 | -6.05* | 48.7 | 47.70 | -2.95* |
| | sd | 0.57 | 0.47 | | 2.09 | 2.26 | | 2.07 | 2.19 | |
| | N | 83 | 78 | | 83 | 77 | | 83 | 76 | |

Table 2.6. (continued)

| | | Mass | | | Wing chord | | | Tail length | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Veracruz | Belize | *t* | Veracruz | Belize | *t* | Veracruz | Belize | *t* |
| American Redstart | mean | 7.33 | 6.93 | -3.52* | 61.05 | 58.11 | -6.92* | 55.44 | 53.71 | -3.70* |
| | sd | 0.52 | 0.50 | | 1.74 | 2.04 | | 1.9 | 2.13 | |
| | N | 50 | 34 | | 50 | 31 | | 50 | 28 | |
| Worm-eating Warbler | mean | 12.22 | 12.27 | 0.25 | 67.03 | 64.85 | -4.11* | 48.79 | 46.76 | -3.79* |
| | sd | 0.77 | 0.80 | | 2.36 | 1.86 | | 2.09 | 2.22 | |
| | N | 34 | 31 | | 34 | 31 | | 34 | 31 | |
| Ovenbird | mean | 17.29 | 17.44 | 0.56 | 73.9 | 70.28 | -7.89* | 53.48 | 50.88 | -6.00* |
| | sd | 1.59 | 1.25 | | 2.5 | 2.69 | | 2.35 | 2.50 | |
| | N | 110 | 44 | | 110 | 43 | | 110 | 42 | |

Table 2.6. (continued)

| | | Mass | | | Wing chord | | | Tail length | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Veracruz | Belize | *t* | Veracruz | Belize | *t* | Veracruz | Belize | *t* |
| Kentucky Warbler | mean | 12.44 | 12.77 | 1.87* | 65.83 | 63.59 | -5.33* | 47.72 | 45.88 | -4.69* |
| | sd | 1.01 | 1.11 | | 2.45 | 2.55 | | 2.11 | 2.62 | |
| | N | 87 | 60 | | 87 | 59 | | 87 | 59 | |
| Hooded Warbler | mean | 9.48 | 9.41 | -0.61 | 63.26 | 61.55 | -4.10* | 54.34 | 54.64 | 0.82 |
| | sd | 0.71 | 0.62 | | 2.5 | 2.22 | | 2.24 | 1.80 | |
| | N | 97 | 50 | | 97 | 51 | | 97 | 50 | |

* $P < 0.05$.

Table 2.7. Fattening trends in autumn Nearctic-Neotropic migrants from study sites in North America.

| Species | Minnesota[1] | Lake Erie[2] | Veracruz[3] | Belize[4] |
|---|---|---|---|---|
| Red-eyed Vireo | 0 | 0 | + | + |
| Veery | | - | | 0 |
| Swainson's Thrush | + | + | | + |
| Wood Thrush | | | 0 | - |
| Gray Catbird | - | + | + | + |
| Magnolia Warbler | + | + | + | + |
| American Redstart | + | + | + | + |
| Worm-eating Warbler | | | +[5] | + |
| Ovenbird | - | + | 0 | 0 |
| Northern Waterthrush | + | + | | + |
| Kentucky Warbler | | | + | + |
| Common Yellowthroat | + | + | | - |
| Hooded Warbler | | | 0 | 0 |
| Wilson's Warbler | | + | + | |
| Indigo Bunting | | | | + |

[1]Winker et al (1992a,b).

[2]Dunn (2001).

[3]Winker (1995a).

[4]This study.

[5]Worm-eating Warbler from Veracruz had significant gains in fat scores, but no trend in condition indices or mass.

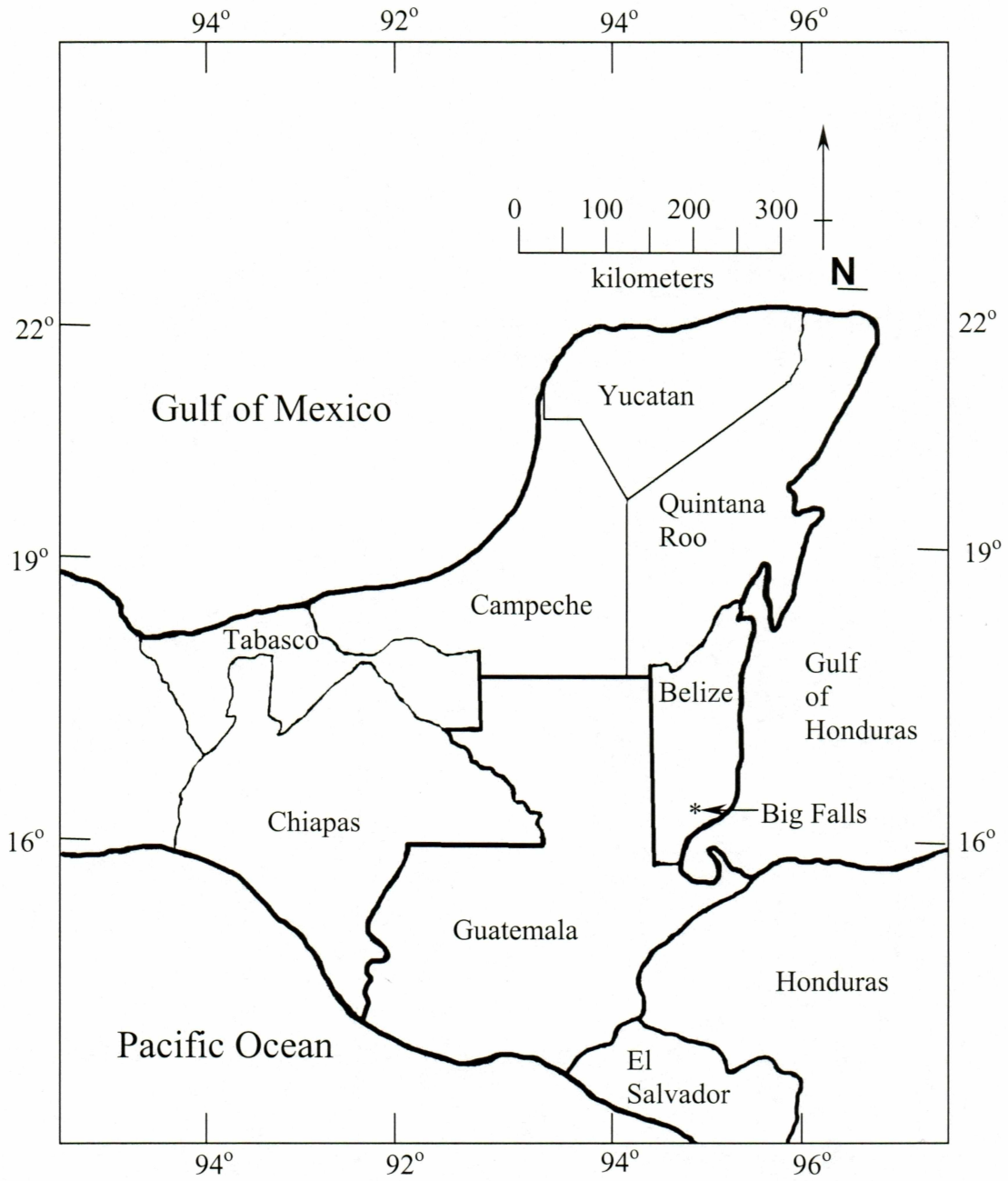


Figure 2.1. Yucatan Peninsula, Gulf of Honduras, and Belize study site (Big Falls).

# GENERAL CONCLUSION

My studies have shown that daily fattening occurs in large numbers of transient Nearctic-Neotropic migrants in the southern Yucatan, and that the lowland forests in the region are important to these migrants as a place to deposit fat. There appear to be different migration strategies among species, as shown by the variability in the degree of fat deposition among species, and because some species arrived at the site already carrying substantial fat. Efforts to conserve and manage these migrants should not overlook the importance of every phase of their annual cycle, including migration and the importance of high quality stopover sites.

The response of resident species to Hurricane Iris was complex and did not appear to have played itself out one year after the hurricane. However, some generalities can be made. The reaction by the community to this catastrophic habitat disturbance was delayed, with local extirpations and severe population reductions in some species accumulating as time passed. The demolition of the forest habitat favored a community dominated by open-habitat and scrub-preferring species, but many forest-associated species remained on the site, and species richness did not change significantly. Survivors made up a small but important part of the community after the hurricane.